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PLANT ECOLOGY OF THE GRAHAMSTOWN NATURE RESERVE

I. PRIMARY COMMUNITIES AND PLANT SUCCESSION

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(With Plates I — IX)

ABSTRACT

Two hundred south-facing acres of admixed temperate rainforest, heath and grassland, at an altitude of 1,800—2,500 ft., on quartzite-derived soils in the Grahamstown hills, Eastern Cape Province, South Africa, were dedicated as a Reserve in 1932. This is the first published account of the vegetation. Soils are sandy loams, acid, weakly podsolic with low humus content and non-nitrifying except in forest and a few favoured sites where pH, organic matter and water content are higher. Community types rather than associations are recognised, as there is no firm classificatory basis of Eastern Province associations to which they may be referred. The community types are referred to six physiographic groups, those of ridges and cliffs, dripping rock outcrops, boulder talus, hill slopes, gullies and seeps, and aquatic conditions. For the majority of community types recognised, species lists and subjective frequency values are given. For forest and scrub, data derived from unpublished transect work of 1932 are given. In discussion, evidence is adduced to show that forest is tending to spread. The Raunkiaer life form spectrum for the entire flora of the Reserve (691 spp.) is given. The most interesting feature of this is the high percentage of hemicryptophytes and chamaephytes, despite the dominance of nanophanerophyte heath and of forest over most of the Reserve. A possible reason for this is the very marginal nature of the climate for heath and forest, with a susceptibility to drought and winter fire.

INTRODUCTION

The Grahamstown Nature Reserve consists of about 200 acres of forest, heath and grassland, situated on the south-facing scarp slope of the Grahamstown hills, which rise to a maximum height of 2,535 ft. (760 m.) at the Survey beacon on Dassie Krantz, the highest point of the Reserve (text fig. 1).

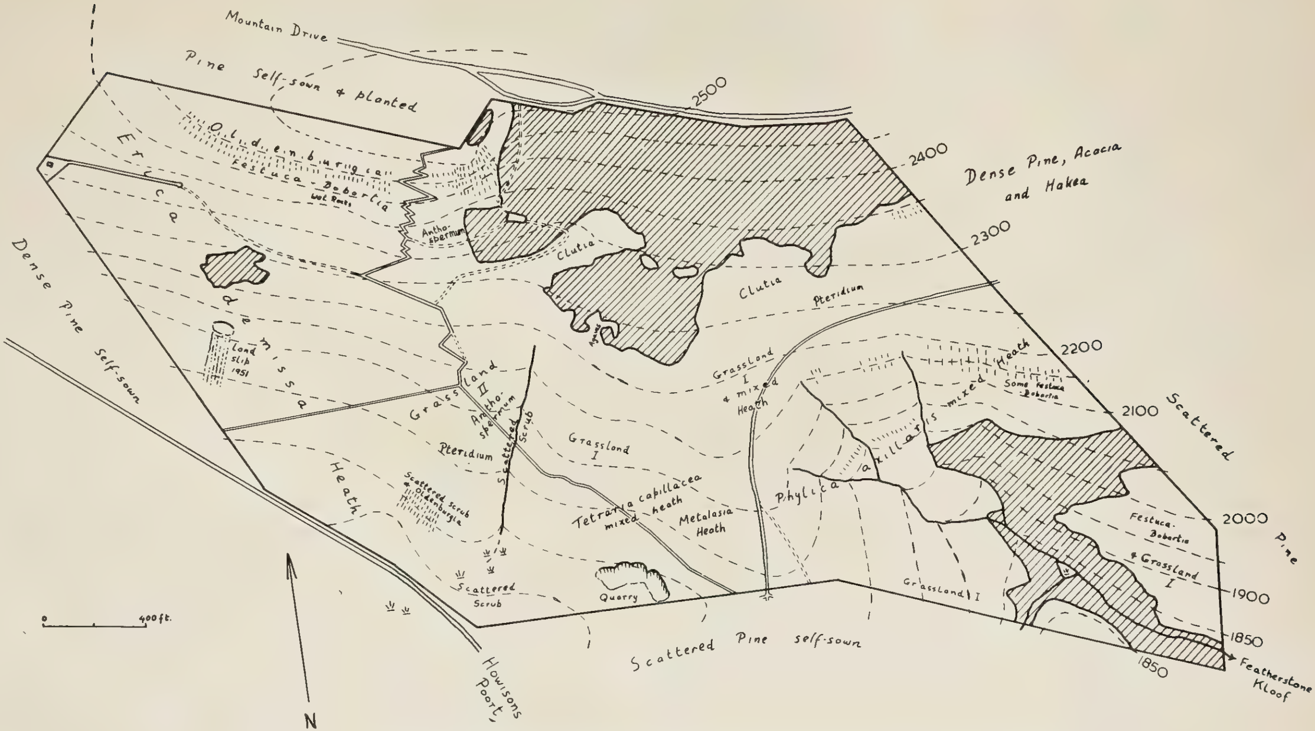
This area was divided into farms shortly after the establishment of Grahamstown in 1812. It was first surveyed in 1827. From this it appears that the Reserve then formed part of the large farm Kowiefontein. This farm was soon subdivided, for the south slope of the ridge, the western end of which forms the Reserve, is shown divided among four owners by 1834 (Cory, 1913). It is clear from this early map that two of these farms, those of Best and Ulyate, bi-sected the Reserve. In 1903 however, ownership of the whole of the ridge reverted to the Grahamstown Municipality, by whom it is still owned as part of the City commonage, grazing rights being leased to individuals. On the 18th April, 1932, through the efforts of the Grahamstown Nature Reserve Society, part of the ridge was declared a nature reserve. The Reserve was not enclosed by fences and firebreaks until some years later, so that some uncontrolled grazing continued for a few years. Conditions of the lease still permit grazing of about 7 head of cattle (theoretically 1 cow to about 30 acres, but not the whole of the area is equally accessible or palatable to grazing cattle), and periodically goats have entered the Reserve. Nonetheless, grazing must have been relatively light for about 25 years.

The vegetation of the Reserve was under observation from 1948 to 1952, and again during 1955 and 1956. Some unpublished data collected at the time of establishment of the Reserve (Liebenberg, 1933; Scott, Norval and Liebenberg, 1933) and photographs held by the Botany Department, Rhodes University, were also studied. These make possible a certain degree of comparison of the state of the vegetation over the twenty-five year period.

GEOLOGY AND TOPOGRAPHY

The hilly, almost mountainous region of Central Albany is formed mainly of Witteberg quartzites and is an extension of the Zuurberg Range further to the west, continued into Albany as the Highlands Range and the Grahamstown Hills, which end at Manleys Flat some 8 miles east of Grahamstown. The Grahamstown Hills are geologically rather uniform in composition. The strata of the quartzites have approximately a 5° dip northwards at this point. Surface silcrete occurs in places on the northerly slopes, but is absent from the scarp side of the range (Mountain, 1946).

Topographically, the part of the Grahamstown Hills on which the Reserve is established forms a unit, bounded on the west by the valley of Howisons



TEXT FIG. 1.—Map of Grahamstown Nature Reserve, based on aerial photography and ground survey, with sketched-in form lines (heights in ft.) and vegetation distribution.

Poort, heading at Waainek, which cuts through the range in a roughly north-south direction, and on the east by a similar lateral valley which the old Kowie Road follows down to the Lower Albany Plain. Into this valley runs Featherstones Kloof to join the Kowie River. A slight col at about 1,900 ft. separates the two.

The Witteberg overlies the Bokkeveld beds which are exposed in the floors of Howisons Poort and Featherstones Kloof, and should underlie the lower end of the Reserve at about 1,800 ft.—1,900 ft. However, they do not appear to be exposed, being covered by a thick layer of large boulders from the Witteberg, some seen in the road cuttings in Howisons Poort, perhaps weighing 50 to 100 tons. Thus the Bokkeveld beds have not participated greatly in soil formation in the Reserve.

The landscape owes its features to the dissection of a once more or less flat surface of late Mesozoic age, the tableland of which has been reduced to a series of ridges with a general height of 2,400—2,500 ft. Drainage is in the main antecedent, but the landscape is moderately young—the valleys being steepsided and the spurs of adjacent hillsides interlocking. These features must be due to the uplift of the land at the end of the Pliocene, estimated to have been about 1,000 ft., which has rejuvenated the river systems.

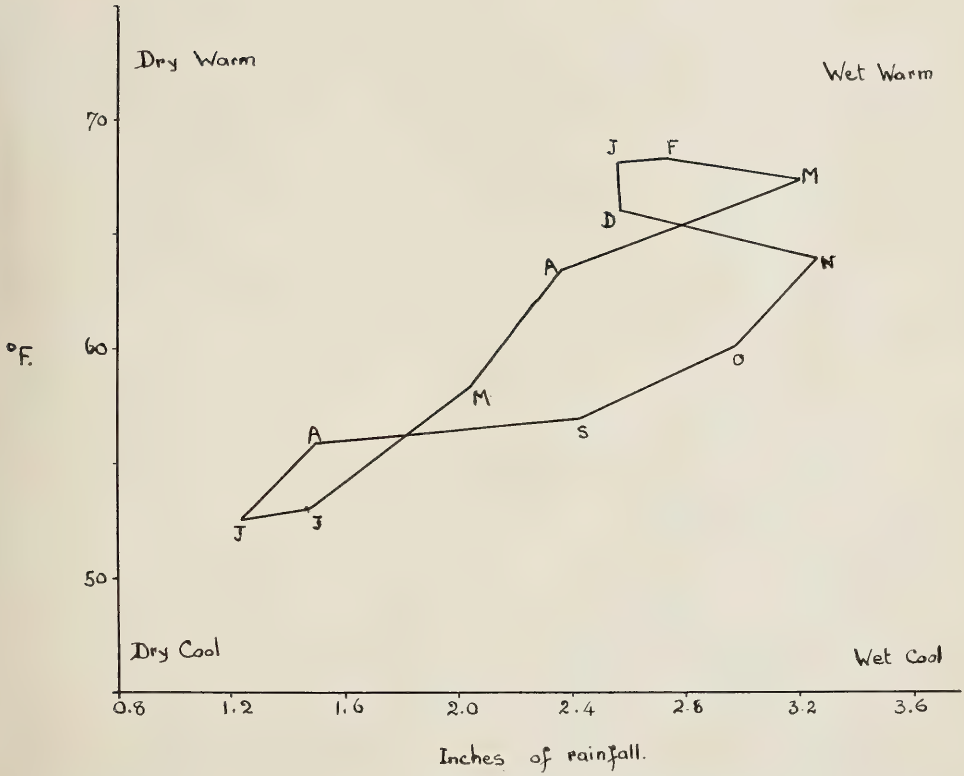
The Witteberg is divided into harder and softer strata, and as these lie nearly horizontally at this point, denudation following the rejuvenation has resulted in an uneven topography, the hard greyish-white quartzites giving rise in places to cliffs or reef-like ridges, or else steep slopes with numerous rock outcrops. At other levels a softer brown ferruginous and sometimes micaceous sandstone has given rise to gentler slopes, mostly vegetation- and soil-covered and lacking outcrops, but sometimes covered with shallow soils exposing surfaces of small sandstone fragments, probably the result of former soil erosion.

Small gullies or larger kloofs have cut back into the hillsides laterally, waterfalls often originating where they cross the harder strata. These kloofs are probably the product of the same Plio-Pleistocene land elevation.

Very little aggradation occurs within the mountain area; although most of the streams have conglomerate-like deposits of Witteberg boulders and pebbles along their banks, alluvial plains of any size are not formed until the plain of Lower Albany is reached.

CLIMATE

It is a pity that meteorological data have never been kept for the Reserve. In lieu of these, a climogram for Grahamstown is presented (text fig. 2), from which it can be seen that a cool, rather dry winter usually alternates with a warm, moderately moist summer. The spring and autumn months appear to be the periods most suited to plant growth. More detailed data are given by Dyer (1937) and Liebenberg (1933). It is well known that in South Africa, climatic conditions can vary surprisingly over a small area, and while the Grahamstown meteorological station is only three miles away, the Reserve, owing to its prominent southerly slope and higher altitude and the fact that it faces the winds from the sea, is cooler and probably wetter than Grahamstown.



Text Fig. 2.—Climogram based on mean monthly rainfall and temperature figures for Grahamstown.

In winter, parts of the Reserve remain in shadow throughout the day, others for a large part of it. Dew appears to be heavier and lies longer. Mist, which seldom reaches Grahamstown, often lies on the ridge. It is probable, but not certain, that the rainfall on the south-facing slope is slightly higher than in Grahamstown, which may suffer from a slight rainshadow effect. It is quite certain, however, that aspect plays an important part in the delimitation of plant communities on this ridge. Increased exposure to wind must to some extent nullify the effect of a better effective rainfall as the crest is approached.

SOILS

TABLE I

MECHANICAL ANALYSIS OF GRAHAMSTOWN NATURE RESERVE SOIL, MOIST HEATH TYPE

	Gravel	Coarse sand	Fine sand	Silt	Clay	Loss on ignition	Moisture Equiv.
Percentage	6	32	29	7·5	27·5	13	22

Moisture equivalent determined by Bouyoucos method.

TABLE II

CHEMICAL ANALYSES OF WITTEBERG QUARTZITE SOILS (ALBANY DIVISION)

	Per-centage	Locality	Notes	Analyst
P_2O_5 ..	0·0149	"Near Grahamstown"	Mean of 64 determinations on 1/40 acre plot. HCl extract, (?) total salts	Barker & Steyn 1956
N	0·1016			
K_2O ..	0·134			
P_2O_5 ..	0·0014	Westhoe, Highlands	Mean of two determinations from adjacent camps. N/20 HCl extract, available salts.	Henrici, 1934
N	0·112			
CaO ..	0·125			
pH				
Heath ..	5·0—5·9 (5·6)	Grahamstown Nature Reserve	Mode and range of 15 determinations	Author's data
Grass ..	5·8—6·0 (5·9)		Mode and range of 6 determinations	
Forest ..	6·1—6·6		Range of 3 determinations	

The soils of the Reserve are derived from the slow-weathering parent Witteberg rock. As such they are rather sandy, acid and poor in most nutrients, especially phosphate, calcium and nitrogen. Henrici (1934) considered phosphate to be usually more limiting than nitrogen in Albany soils. The soils are sandy loams, bordering on sandy clay loams (Table I), with low to moderate organic content (loss on ignition 4 to 6% under heath rising to 10 to 15% under forest), with a pH of 5·0 to 6·6, averaging 5·7 (Table II). These soils rather easily lose crumb structure and become compacted and erodable. No part of the Reserve has accumulated a deep soil, owing to the slope. The profile is more or less immature, or even skeletal. The depth may be as little as 3 inches and is rarely more than 2 ft. (phot. 1). There is generally a layer of unweathered quartzite boulders over the solid rock. Near the top of the ridge the surface consists in places of blocks of scarcely weathered quartzite, the faces of which bear only lichens, while vascular plants have colonised the soil pockets between the blocks. Owing to the high relief and sandy soil, drainage is rapid. After heavy rain, streams fed by small springs carry off the water for a few days, but soon dry up. The soils are not highly leached, as is shown by the weak development of soil horizons, even in the deepest profile seen, about 4 ft. Probably prolonged gravitational creep and descent of rock material from higher up the hillside is replenishing the loss by leaching. It is noticeable that even under well-developed and apparently stable forest, the surface soils contain coarse gravel and occasional small boulders. Nevertheless, the soils are weakly podsolised and classifiable (Van der Merwe 1941) as grey podsolics, the podsolisation even in the deeper profiles sometimes showing only as a weak accumulation of the clay fraction, at a depth of about 12 inches in a vestigial B horizon without change in soil colour.

The nitrifying ability of samples from several vegetation types was determined by the diphenol sulphonic acid method of Olsen (1923) (Table III). The percentage change on storage (not the absolute value) defines the power of nitrification or denitrification. It was found that below 2 p.p.m. the method was not very reliable, owing to a slight background colouring of the samples. The *Festuca-Bobartia* heath and the four *Erica* heath samples are remarkably similar except in water content. Among the nitrifying samples, it is interesting to see the majority of the grassland samples. They are not otherwise differentiated, water content, loss on ignition and pH being comparable with the non-nitrifying samples. In this group too, comes the *Anthospermum-Rubus* community. The forest soil, on the other hand, has high pH, water content and loss on ignition, and is well differentiated from the other types. The *Adenocline-Zantedeschia*-Sedge community below Dassie Krantz calls for special comment as being the only sample with high initial nitrate. Its nitrifying ability is not outstanding considering this high initial value, which is probably due to nitrogen contributions by the colony of coneys (*Procavia*) living in the talus below the krantz.

Table III

NITRIFICATION IN GRAHAMSTOWN NATURE RESERVE SOILS

	p.p.m. NO_3		Percentage H_2O	Loss on ignition	pH
	Immediate	After 30 days			
1. *Non-nitrifying soils*					
Unburnt *Erica* heath, western end of Reserve (*a*)	0·9	1·5	10·21	4·17	5·54
(*b*)	2·7	0·7	10·52	5·13	5·56
(*c*)	2·9	0·6	14·17	5·99	5·59
(*d*)	1·0	1·4	18·94	6·63	5·53
Metalasia muricata heath with much grass ..	3·7	0·8	19·32	3·88	5·89
Tall tussock grassland ..	2·3	1·2	15·21	4·53	5·94
Festuca-Bobartia heath with *Phylica*	1·0	1·8	21·78	6·12	5·65
2. *Nitrifying soils*					
Stream bed community ..	7·6	37·8	33·72	8·95	5·62
Anthospermum-Rubus community overlooking preceding	1·6	11·8	17·47	3·98	6·02
Adenocline-Zantedeschia Sedge community below Dassie Krantz	26·8	84·7	26·22	4·75	6·13
Forest adjacent to preceding	5·5	47·0	29·79	9·80	6·16
Small forest patch, western end	5·1	68·6	27·76	12·84	6·62
Low tussock grassland, *Digitaria*	0·7	8·3	17·09	4·83	5·83
Grassy clearing in forest	4·3	41·9	17·45	2·67	5·96
Low tussock grassland, *Sporobolus* and *Trifolium*	1·9	7·8	19·21	3·20	6·02

THE VEGETATIONAL HISTORY OF THE RESERVE, AND PLANT SUCCESSION

The vegetation of the north and south-facing slopes of the Grahamstown Hills differs strikingly, and this difference is probably of long standing. Paintings of about 1840 show the north-facing slopes grass-clad and bare of trees, and while no pictorial record exists clearly showing the condition of the south slopes, the indication is that they have for a long time borne low forest—at least in the more sheltered kloofs—and heath. Photographs show pine plantations already established on the north slopes as far as the crests by 1900, and some selfsown saplings already developing. These trees, together with *Acacia longi-*

folia (Australian Wattle) now cover the greater part of the north slopes near Grahamstown, and the original flora can only be inferred by comparison with the still grass-clad slopes further west and east. Photographs show the western end of the south slope (Howisons Poort and Waainek) to be heath heavily invaded by pines by 1930. Pines, *Acacia longifolia* and some *Hakea acicularis* are still encroaching on this slope and on the farther ridge. *Pinus pinaster* is especially fast growing, and enjoys widespread wind dispersal of its abundant seed, so that it spreads rapidly from its centres at the top of the ridge. *P. halepensis* also occurs but is much less frequent. The major effect of pines has been to lower soil pH, accelerate podsolisation and to modify the flora (Seagrief 1950) and the soil fauna (Watts 1951).

One of the first concerns of the Nature Reserve Society was to eradicate the invading species. Clearing was achieved by volunteers, partly by felling and uprooting and partly by use of fire. Stumps of well-grown pines up to 12″ diameter were common in the heath prior to the most recent burnings, and all those examined bore the marks of former burning, which probably took place at about the time of establishment of the Reserve. As the oldest plants of *Erica demissa* examined were about 20 years old, it is likely that at least a good deal of the heath examined between 1948 and 1956 was first established shortly after this burning.

Physiographically considered, the vegetation occupies a land surface probably of Late Mesozoic origin, rejuvenated and dissected in the Late Tertiary. Bearing in mind this geomorphological history, six chief categories of surface for primary succession are recognised, each possessing a distinct plant community grouping, related to the physiographic processes whereby the surfaces originated.

(1) **Steep rocky slopes, cliffs and ridges,** e.g. Dassie Krantz. Small valleys which enter the main ones at right angles may eventually create cliffs, facing more or less east or west, at the points where they cut through the harder bands. Where hard horizontal layers of quartzite occur, erosion results in their exposure as south-facing outcrops; where the larger valleys are cut down well below the level of these they form cliffs or ridges, running more or less east-west. Dassie Krantz however falls into neither of these groups. It represents a sudden step forward in the general line of the scarp as if faulting had occurred. However, no clear geological evidence of faulting is present. *Community types:* predominantly chasmophytic communities.

(2) **Wet rocks or dripping rock ledges.** (*a*) Where insequent streams cut back over a harder band of rock, a small waterfall originates. It may be supposed that at a later stage of dissection, a kloof will form in these places with a cliff on either side, while the waterfall may persist as long as the stream flows over the

hard stratum. Within the Reserve no examples of this type occur, though they are not uncommon in the Albany Ranges. *Community types:* absent in the Reserve.

(*b*) Where seepage of water occurs along joint-planes, small springs often occur and gravitational slumping of the wet soil may expose the underlying rock. In this way a wet rock surface originates, from the surface or top of which water drips at least periodically. The continued action of spring water may start a gully below the rock outcrop. Such an outcrop will only persist if the rock is of harder type. *Community types:* moss mats and wet heath. The difference between (*a*) and (*b*) is perhaps slight. It is probable that on the south slopes of the range gullies have arisen through water erosion from wet flushes and seeps, as well as by the cutting back, or stream head erosion, of pre-existing gullies from below.

(3) **Boulder talus below cliffs.** Below the larger cliffs a boulder talus accumulates in which *Procavia*, the coney or dassie, makes its home. *Community types:* chasmophytic, herbaceous sciophytes and scrub.

(4) **Weathered hill slopes.** Softer rock horizons are weathered as they outcrop, and this weathered material forms the greater part of the hill slopes. Locally, gravitation of partly weathered rubble or of soil results in slow creep down the hillsides, or earth slips, but large landslides must be rare. *Community types:* main grassland and heath communities of Reserve, some forest.

(5) **Areas of drainage concentration**—banks of gullies, flushes and slumps. Areas of increased soil water content can arise in several ways: (*a*) by the issue of water from the rock into the subsoil forming a flush or seep; (*b*) consequent slumping of the wet surface soil or rock debris, producing slight hollows with drainage impeded by the lip. In the more extreme cases an earthslip may result (phot. 17); (*c*) the conformation of the ground causing channelling of water drainage into lines of sub-surface flow, which tend to form gullies; (*d*) deepening and cutting back of existing gullies; (*e*) outcrops of impermeable strata leading to perched water tables above them, often associated with shrub growth. *Community types:* Hygrophytic heath and grassland, and some scrub and forest.

(6) **Areas of open water and silting.** Large bodies of water do not accumulate and small bodies do not persist long. Nonetheless, along the lower parts of the two main streams draining the Reserve, flow is sufficiently perennial for marshy conditions to develop. *Community types:* hygrophytic heath, grassland and sedge with some helophytes but no true hydrophytic communities.

Owing to the slow rate of origin of new bare areas and the slow-weathering nature of the Witteberg, it is hard to identify successional stages of seres on these surfaces; moreover, the sere on dry rocks proceeds far more slowly than that on wet rock or talus, and the sere on the slower weathering harder strata must proceed more slowly than that on the more rapidly weathering hill-slopes. Thus on cliffs, vegetation may remain unstable for a long time, even after a scrub of forest species has become established on the cliff face, while on the gentler slopes a relatively stable heath of leptophyllous ericoid species develops as soil accumulates round and above the variously shaped and sized boulders, which gradually weather into smaller particles. Initial stages of plant succession are few and often mixed in a mosaic with later stages, forming a cosere (Clements 1916) which is difficult to interpret.

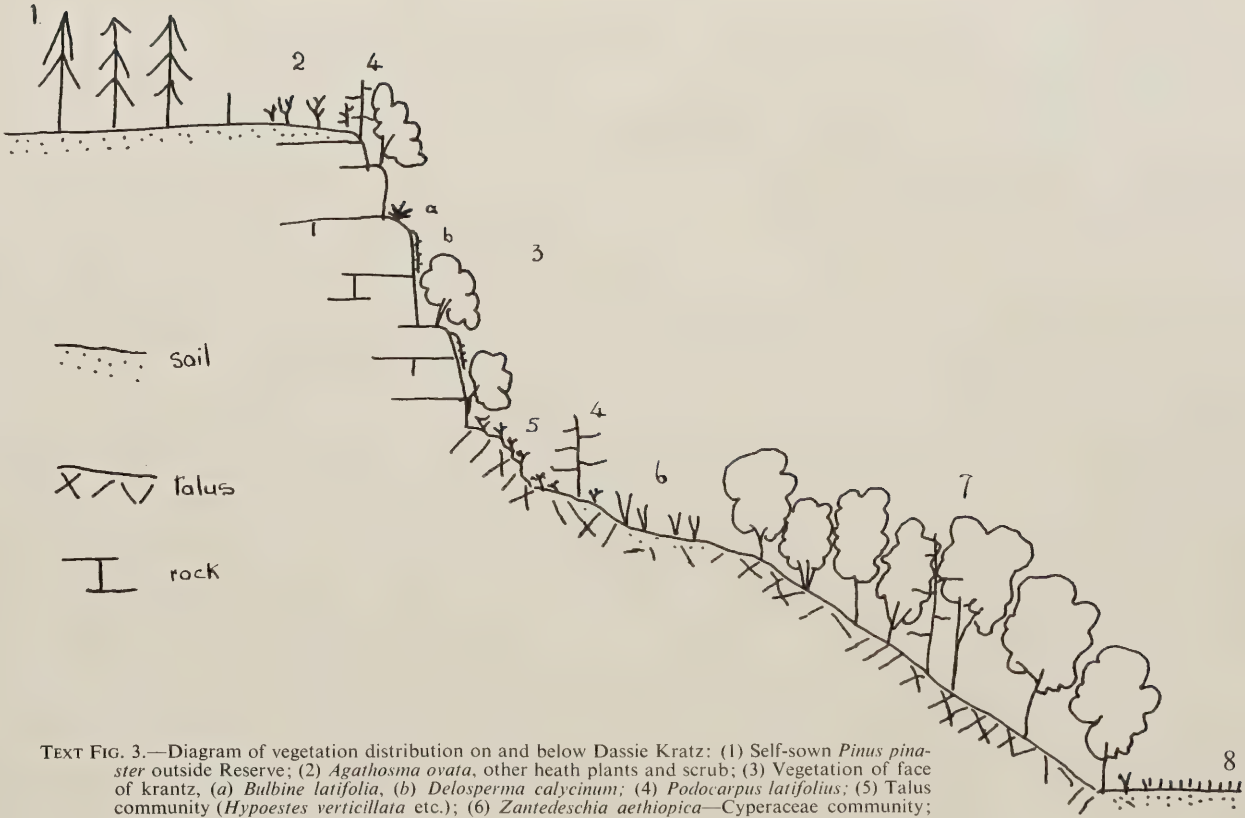
TYPES OF VEGETATION PRESENT IN THE RESERVE

The term "vegetation-type" or "community-type" is used here rather than "association" because in an area of such small extent, and in the absence of any comparison with other parts of the Grahamstown Hills and other Witteberg ridges, it is difficult to distinguish between widespread and recurring vegetation types and those that are purely local or fortuitous.

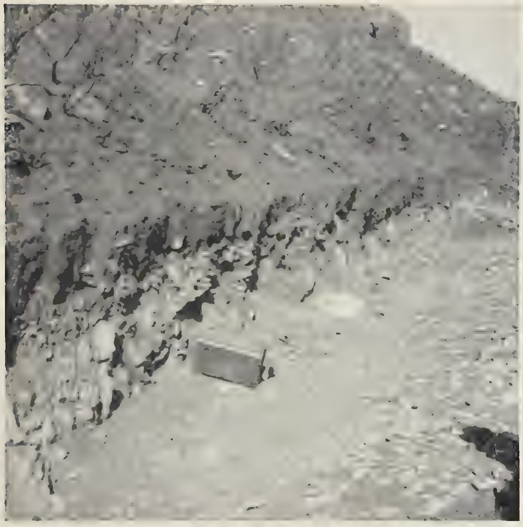
(1) Community Types of Steep Rocky Slopes, Cliffs and Ridges

Dassie Krantz is the only large rock face on the Reserve. The vegetation of small outcrops is only considered insofar as it differs from that of Dassie Krantz. The top of Dassie Krantz stands 2,535 ft. above sea-level. The foot of the krantz is about 120 ft. lower, the greater part of this drop being in the form of more or less vertical drops of up to 30 ft. at a time, separated by shelf-like steps or ledges. Despite the steepness, a large part of the krantz is vegetated. A sketch section of the krantz is given in text fig. 3.

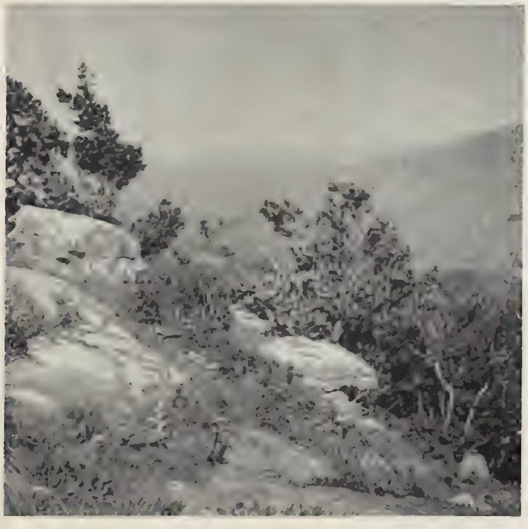
The vertical rock faces on the krantz bear mainly *Usnea* and *Ramalina* spp. *Hypnum cupressiforme* rarely becomes established on bare rock, but is frequent on ledges with a minimum of soil. Minute crevices may contain *Lycopodium gnidioides*. At the top of the krantz, *Crassula rosularis*, *Disperis micrantha*, *Ficinia* sp., *Holothrix lindleyana*, *H. villosa* and *Othonna carnosa* form definite crevice soil communities, mainly of rosette plants, corresponding to Warming's (1909) "rosette chasmophytes". *Bulbine latifolia* is a larger and more robust succulent rosette plant, which seems to form distinct communities. It may possibly be successional to the smaller rosette communities, but this has not been clearly shown. On these ledges with shallow soil, scrub of *Ficus burt-davyi*, *Allophylus decipiens* and *Pleomele hookeriana* seem to become established directly in the wake of the pioneers.



TEXT FIG. 3.—Diagram of vegetation distribution on and below Dassie Kratz: (1) Self-sown *Pinus pinaster* outside Reserve; (2) *Agathosma ovata*, other heath plants and scrub; (3) Vegetation of face of krantz, (*a*) *Bulbine latifolia*, (*b*) *Delosperma calycinum;* (4) *Podocarpus latifolius;* (5) Talus community (*Hypoestes verticillata* etc.); (6) *Zantedeschia aethiopica*—Cyperaceae community; (7) Evergreen forest; (8) Grassy clearing.



Phot. 1.—Soil profile on Nature Reserve (burnt area): shallow A and B horizons not strongly differentiated, passing into C horizon with angular rock fragments, a product of gravitational transport at an earlier period of erosion. Note also similar surface boulders, resulting from more recent gravitational movement.



Phot. 2.—*Oldenburgia* and *Podocarpus latifolius* together at upper western side of Dassie Krantz. In foreground open "ridge" vegetation of *Carpobrotus edulis* and small herbs and shrubs in shallow soil between flat boulders covered with encrusting lichens.

Plate I

Table IV

FLORA OF THE FACE OF DASSIE KRANTZ

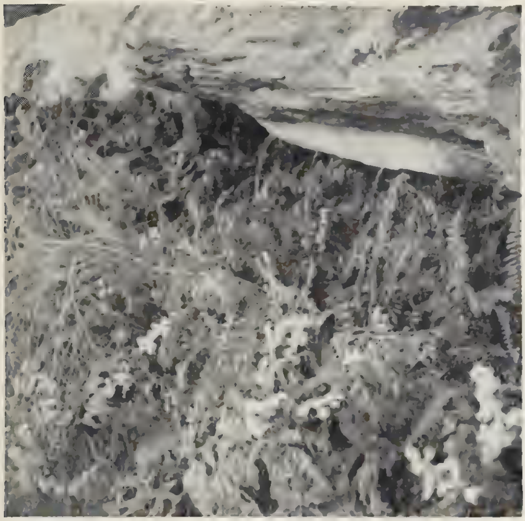
Allophylus decipiens
Bulbine latifolia
Chenopodium sp.
Coccinea quinqueloba
Crassula lactea
C. nemorosa
C. perforata
Delosperma calycinum
Ficus burtt-davyi
Grewia occidentalis
Haemanthus albiflos
Lycium ferocissimum
Melothria punctata
Pleomele hookeriana
Podocarpus latifolius (mainly at edges)
Senecio angulatus
S. mikanioides
Lichens
Leptogium sp.
Parmelia hottentotta
Parmelia sp.
Ramalina sp.
Usnea sp.

Vegetation of other steep dry rocks is similar to Dassie Krantz, but two distinct communities occur. (*a*) Where the slope is at all northerly, as in one or two places along the ridge west of Dassie Krantz and on one of the spur ridges lower down, *Crassula falcata* and *Pellaea calomelanos* are present. These species were never found on south-facing slopes. (*b*) Where the outcrop of rock forms a horizontal reef-like exposure along the hillside, this is marked by lines of the tree Composite *Oldenburgia arbuscula*, which may be regarded as physiognomically the dominant of a distinct community-type. *Oldenburgia* is absent from the face of Dassie Krantz itself, although common at the sides and just above the cliff (phot. 2). This may be due to instability of the cliff

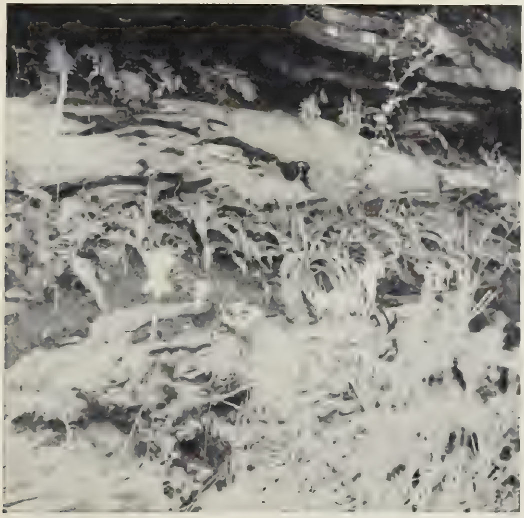
Table V

FLORA OF OLDENBURGIA COMMUNITY

Adenocline bupleuroides	o	*Ficinea indica*	o–f
Agapanthus africanus	l.c.	*Ficus ingens*	r
Amphithalea phylicoides	v.r.	*Grewia occidentalis*	f
Aspalathus chortophila	o	*Haworthia monticola* var. *albanensis*	o
Asparagus sarmentosus	o–f	*Knowltonia capensis*	o
Bulbine latifolia	f	*Lampranthus spectabilis*	f
Caesia eckloniana	r	*Montinia caryophyllacea*	o–f
Cineraria saxifraga	c	*Muraltia macowani*	l.c.
Crassula cultrata	c	*Oldenburgia arbuscula*	d
C. falcata	l	*Osteospermum junceum*	o–f
C. lactea	o–f	*Othonna carnosa*	f
C. obvallata	o–f	*Pellaea calomelanos*	l
Delosperma britteniae	o	*Rafnia elliptica*	o–f
D. calycinum	o–f	*Rhoicissus dimidiata*	o
Ehrhardta erecta	o	*Rhyticarpus difformis*	o
Euclea lanceolata	o–f	*Scilla lancaeafolia*	o–f
Ficinea c.f. *elongata*	f	*Senecio crassiusculus*	o
F. bracteata	f–c	*Streptocarpus meyeri*	o
F. fascicularis	f–c	*Teedia lucida*	r



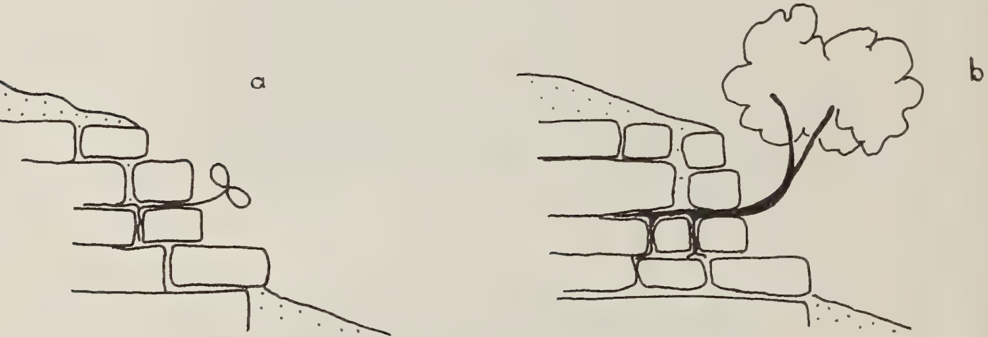
Phot. 3.—*Blechnum australe, Helichrysum petiolatum, H. orbiculare, Ficinea gracilis* and *Clutia affinis* in shelter of overhanging rock ledge.



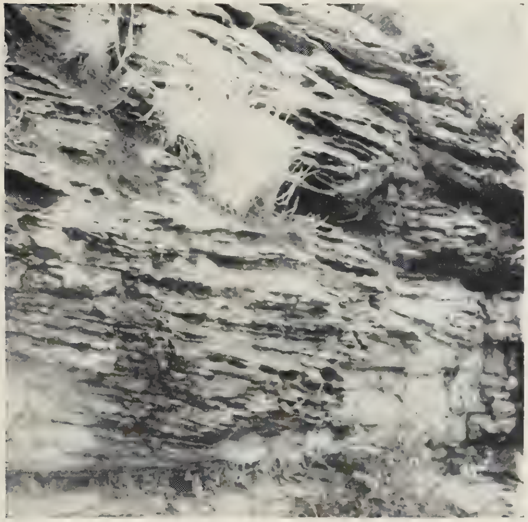
Phot. 4.—Continually moist south-facing rock outcrop. Note crevice flora of *Blechnum australe*, moss mats, and *Hypoxis obliqua, Senecio rigidus* and *Ursinea anethoides.* A small plant of *Rapanea melanophloeos* is present.

PLATE II

face. Most mature trees of *Oldenburgia* have trunks out of perpendicular. Several instances of collapse of old trees were noted. It seems that as the tree becomes mature, a combination of its own weight and the dislocation of rock slabs by its roots ultimately results in falls of parts of the rock face and of the tree, as in the series of diagrams (text fig. 4) and phot. 16, leading to a cyclical development.



Text Fig. 4.—Diagram of erosional cycle associated with *Oldenburgia arbuscula:* (*a*) Juvenile, (*b*) Mature, (*c*) Over-mature, (*d*) Collapse stage.



PHOT. 5.—Same outcrop as in phot. 4, but 50 m. farther west, here only periodically wet. Flora is mainly *Agrostis bergiana* and *Restio triticeus*, with dark mats of *Frullania c. f. lindenbergii*, other Bryophytes and Ferns scarce, and luxuriance of vegetation at base of outcrop restricted.

PHOT. 6.—Flora of wet rock surfaces—mats of *Campylopus* sp. and *Breutelia*, with *Drosera cuneifolia*, *Utricularia capensis* and seedlings of *Erica demissa* and *E. chamissonis.*

PLATE III

(2) Community-types of wet rock outcrops

The development of vegetation on wet rock outcrops seems to depend on the degree of insolation (steep or overhung outcrops have a more sciophilous vegetation), and the volume and periodicity of water flow. The chemical composition of the water has not been closely investigated, but is probably fairly uniform. A complete range between wet and dry rock faces exists and thus a complete range of community-types between the xerarch types described above and the wettest. However, only a few of these appear within the Reserve. Three such sites, somewhat contrasted, but with some common features, are shown in phots. 3, 4 and 5.

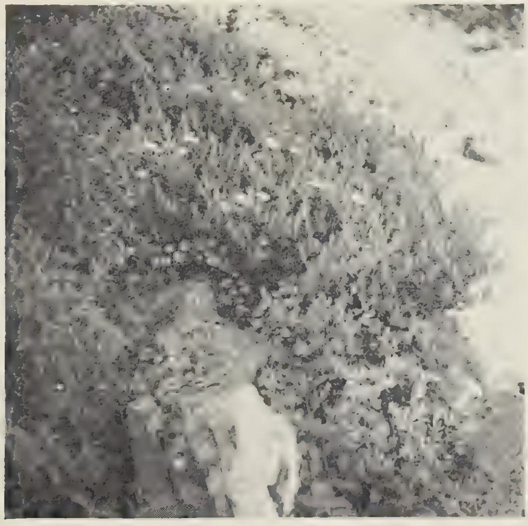
Blechnum australe and *Helichrysum orbiculare*, especially the former, constitute a sciophilous community-type, being quite typical of sites where flat ledges of rock project, forming a shaded recess which can only receive direct sunlight when the sun is low in the early morning. No site was observed where late evening sun entered.

Table VI

FLORA OF DRIPPING ROCKS

Agrostis bergiana
Alepidea capensis
Anthospermum aethiopicum
Athrixia crinita
Berzelia intermedia
Bobartia burchellii
Chironia melampyrifolia
Clutia alaternoides
C. heterophylla
Danthonia cincta
Disa sagittalis
Drosera cuneifolia
Erica cerinthoides
E. chamissonis
E. demissa
Festuca costata
Ficinia fascicularis
F. cf. *gracilis*
Gnidia styphelioides
Helichrysum felinum
H. orbiculare
H. petiolatum
Hypoxis obliqua
Leidesia obtusa
Myrsine africana
Ornithogalum bolusianum
Osteopermum junceum
Pelargonium ribifolium
Pinus sp. (dead, burnt sapling)
Psoralea pinnata
Rapanea melanophloeos (sapling, one only)
Restio triticeus
Sebaea hymenosepala
Satyrium sp. (? *membranaceum*)
Senecio concolor
S. pterophorus
S. purpureus
Tetraria capillacea
T. cuspidata
Themeda triandra
Ursinia anethoides
Utricularia capensis
Pteridophyta
Blechnum australe
Bryophyta
Anthoceros sp.
Breutelia sp.
Bartramidula globosa
Calypogeia fusca
Campylopus sp. i
C. sp. ii
Fissidens glaucescens
Frullania lindenbergii
Lepidozia capillaris
Philonotis androgyna
Trematodon pillansii

Phot. 7.—*Erica chamissonis*, *E. demissa*, young plants of *Disa sagittalis* and *Helichrysum orbiculare* on *Campylopus* mat. Note covering by dry crust of Blue-green algae (Chroöcoccales) on lower right—beginning of degeneration of the mat.



Phot. 8.—Dassie Krantz boulder talus. *Lampranthus* sp. rooted in crevices and straggling over rocks, *Plectranthus strigosus* and *Hypoëstes verticillaris*. Note thallose lichens on rock surface.

Plate IV

Plant succession on a ledge in a moist outcrop community (phot. 4) appears to start with the development of a slime of blue-green algae over which moss mats of *Campylopus* sp. and *Breutelia* sp. usually develop. In these mats *Drosera* and *Utricularia* become established, followed by *Agrostis bergiana*, *Alepidea* and seedlings of *Erica demissa*, *Berzelia intermedia*, *Ursinia anethoides*, etc. (Table VI). However, the moss mats often become dried out and moribund, with a horny pellicle consisting of a mixture of gelatinous blue-green algae, mainly *Gloeocapsa* spp. (phot. 6 and 7). Such mats are often washed off the ledge by the first following heavy rain, adding to the depth of soil on the slope below the ledge. Succession then recommences on the bare rock. Gravitational collapse may also occur at the stage of heath establishment, and no stages later than this were observed. Phot. 5 is of a rock surface which is only periodically wet. The flora is much less luxuriant, consisting mainly of *Agrostis bergiana* and *Restio triticeus*. *Blechnum* and Bryophytes, except *Frullania lindenbergii*, are scarce.

(3) COMMUNITY-TYPE OF BOULDER TALUS

There is only one at all extensive talus slope in the Reserve; this is at the base and eastern side of Dassie Krantz.

The abundance of climbing and trailing plants (chasmophytes; Warming, 1909, Schimper, 1903) is remarkable. *Clematis*, *Senecio* spp., Cucurbitaceae spp., *Dioscorea* and *Rubus* illustrate the habit well. Even some species which do not normally straggle do so here, e.g. *Grewia occidentalis* and *Fleurya mitis* (phot. 9). Two successions can be traced: that on rock surfaces, which tends to be lichens → xeric mosses → *Crassula lineolata*, *Cineraria saxifraga* or *Lampranthus* sp. (phot. 8, 9); and that in crevices, which seems to be liverwort mats → annual herbs → perennial herbs, ferns and creepers → shrubs and trees. On this slope a number of shrubs and trees have invaded the tangle: *Podocarpus latifolius* seems to be one of the most successful. None of the plants on the talus slope can be described as leptophyllous nanophanerophytes. Thus, under some circumstances the forest species will colonise bare areas via crevices. A part of the woodland, especially below and at the eastern side of Dassie Krantz, seems to have arisen in this manner (see discussion). On top of the cliff, however, leptophyllous nanophanerophytes (mainly *Agathosma* spp.) form a well-marked stage in succession to scrub.

(4) COMMUNITY TYPES OF THE HILL SLOPES

The slope of the Grahamstown Hills varies from 5° to 30° or more. (Slopes greater than 30° are usually more or less rocky or liable to slumping.) These slopes are occupied by a complex and varied vegetation, including forest, heath and grassland, and small areas of stream bank vegetation. Examples

Table VII
FLORA OF THE TALUS BELOW DASSIE KRANTZ

Adenocline acuta
Bulbine latifolia
Carpobrotus edulis
Cerastium capense
Cineraria saxifraga
Clematis brachiata
Coccinea quinqueloba
Cotula heterocarpa
Cotyledon velutina var. *beckeri*
Crassula lineolata
C. marginalis
C. nemorosa
C. spatulata
Delosperma calycinum
Dioscorea sylvatica
Disa sagittalis
Disperis micrantha
Ficinia elongata
Fleurya mitis
Galopina circaeoides
Geranium ornithopodum
Grewia occidentalis
*"*Gymnosporia buxifolia*"
Helichrysum foetidum
H. petiolatum
Hypochoeris radicata
Hypoëstes aristata
Hy. verticillaris
Lampranthus sp.
Leidesia obtusa
Lepidium africanum
Lithospermum officinale
Mariscus owani
Melica racemosa
Myosotis intermedia
Nemesia melissaefolia
Oldenburgia arbuscula
Ornithogalum bolusianum
O. caudatum
Panicum maximum
Peperomia retusa
Plectranthus ciliaris
P. laxiflorus
Plectranthus strigosus
P. thunbergii
Pleomele hookeriana
Podocarpus latifolius
Polycarpon tetraphyllum
Ranunculus multifidus
Rhoicissus cuneifolia
Rubus pinnatus
Rumex sagittatus
Scutia indica
Senecio angulatus
S. deltoideus
S. mikanioides
Solanum nigrum
So. quadrangulare
So. sodomaeum
Stellaria media
Sutera cordata
Sisymbrium capense
Tolpis capensis
Trifolium burchellianum
Vulpia bromoides
Zantedeschia aethiopica
Pteridophyta
Asplenium adiantum-nigrum
A. erectum
A. lunulatum
A. (?) *platyneuron*
Lycopodium gnidioides
Pellaea viridis
Polypodium vulgare
Polystichum adiantiforme
Bryophyta
Aerobryopsis capensis
Bryum capillare
B. sp. aff. *B. rigidicuspis*
Calypogeia fusca
Frullania sp.
Hypnum cupressiforme
Lophocolea bidentata
Plagiochila natalensis
Ptychomitrium crispatum
Triquetrella tristichia

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*W. Marais (Bothalia, 7 (2), 1960, p. 381) includes both *Gymnosporia angularis* (Sond.) Sim and *G. buxifolia* (L) Szysz. in *Maytenus cymosus* (Soland) Exell. I have not seen this paper, and as *G. angularis* on the Reserve is a slightly branched shrub, always found in heath, while *G. buxifolia* is a much branched tree nearly always found in scrub and forest, the two forms being clearly distinguishable, I prefer to identify them by earlier names, not doubting both should be referred to *Maytenus*.

of all these occur in the Nature Reserve. The approximate area occupied by grassland and heath is hard to assess, owing to their occurrence in places in a mosaic. Scrub and low forest occupy about 20% of the area.

(*a*) **Nanophanerophytic heath formation:** *Erica demissa*—mixed heath alliance.

The heath may be divided into a number of communities distinguishable by eye. Certain groupings of species not falling into any of these categories occur, but are too fragmentary and insufficiently well characterised to be named. The major communities are:—

(i) *Erica demissa* heath.
(ii) *E. demissa*—*Phylica axillaris*—other spp. heath.
(iii) *Metalasia muricata* heath.
(iv) *Tetraria capillacea*—mixed dwarf shrub heath.
(v) *Anthospermum aethiopicum* heath.
(vi) *Cliffortia linearifolia* heath.
(vii) *Pteridium* heath.
(viii) *Clutia affinis* heath.
(ix) *Festuca costata*—*Bobartia burchellii* grass-heath.

(i) The *Erica demissa* heath is structurally the most advanced and appears formerly to have occupied a larger area.

The flora is large and as the heath has indistinct margins and occurs in mosaic form with other communities, it is hard to make a list which is inclusive without at once admitting a number of casuals or strays. The following list, which is not complete, comprises most species which regularly occur in mature *E. demissa* heath.

Table VIII

FLORA OF MATURE *ERICA DEMISSA* HEATH

Alloteropsis semialata	f–c	*H. nudifolium*	c–a
Andropogon appendiculatus	o	*H. petiolatum*	l
		H. subglomeratum	c–a
Anisotoma mollis	o	*Hypoxis obliqua*	f
Anthospermum aethiopicum	f–c	*Metalasia muricata*	o–f
		Myrsine africana	r–o
A. lanceolatum	o	*Ochna atropurpurea*	r–o
A. paniculatum	o–f	*O. imbricata* var. *violacea*	f–a
Argyrolobium stipulaceum	o	*Oxalis punctata*	f–a
		O. smithiana	o–f
Berkheya carduoides	f	*Pentaschistis angustifolia*	f
B. decurrens	f	*Pimpinella schlechteri*	o–f
Bobartia burchellii	f	*Pinus pinaster*	r–o
B. indica	l–a	*Polygala ohlendorfiana*	r

FLORA OF MATURE *ERICA DEMISSA* HEATH *cont.*

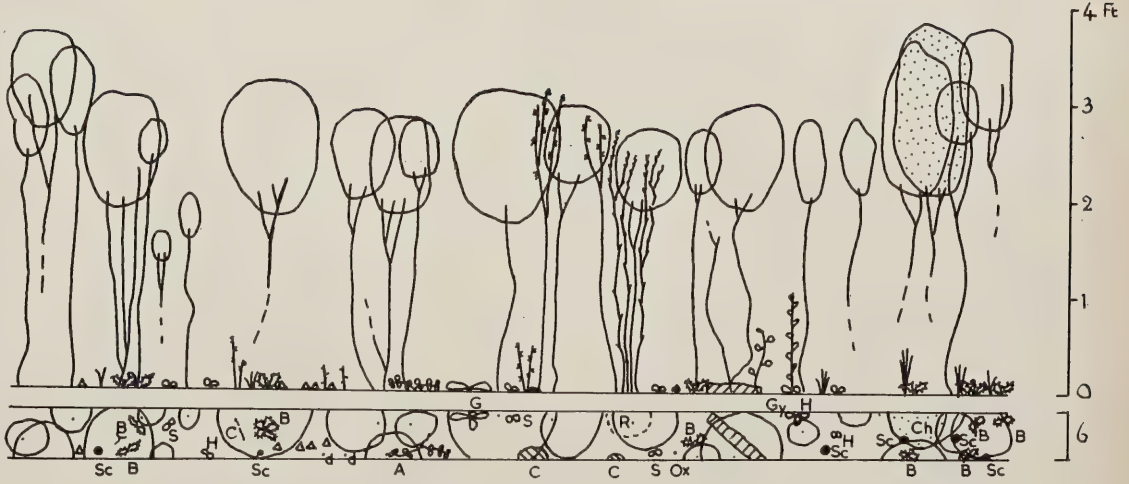
Burchellia bubalina	o
Chaetacanthus setiger	f
Chironia melampyrifolia	r–o
Ch. tetragona	o
Cliffortia linearifolia	c–d
C. repens	o–f
Clutia heterophylla	f
Disparago ericoides	o
Eragrostis curvula	o–f
Erica chamissonis	o–c
E. demissa	a–d
Ficinea stolonifera	o–f
Gerbera viridifolia	f
"*Gymnosporia angularis*"	r–o
Halleria lucida	r
Haplocarpha scaposa	o
Helichrysum appendiculatum	f
H. felinum	f–c
Psoralea spicata	l
Pteridium aquilinum	o–c
Restio sejunctus	o–f
R. triticeus	c
Rhus dentata	r
Rh. eckloniana	o
Rh. fastigiata	o
Rh. lucida	r
Royena pubescens	r–o
Rubus pinnatus	l
Satyrium membranaceum	o
Scabiosa anthemifolia	o-f
Schoenoxiphium sparteum	c
Sebaea sp.	f
Senecio othonnaeflorus	c
Struthiola macowani	o–f
S. parviflora	o
Tephrosia grandiflora	o
Themeda triandra	c–a
Wahlenbergia capillacea	o

Text fig. 5 represents a small portion of a transect in an area of mature *Erica demissa* heath which had not been burnt for about 22 years (that it had been burnt then was shown by the still persisting marks of fire on pine stumps now overgrown by the heath). The mature *E. demissa* forms tall, single-stemmed, narrow-crowned plants about 4—5 ft. in height with stems 1—1½ inches in girth. They comprise about 90% of the plant cover, the rest being made up in the main of *E. chamissonis*, *Cliffortia linearifolia* and *Anthospermum aethiopicum*. In this sample of heath, the only old stand still remaining in the Reserve after the severe 1955 fire, small microphyllous and mesophyllous shrubs, e.g. *Rhus fastigiata*, *Burchellia bubalina* and *Royena* sp., were present. Whether they represent normal constituents of mature heath, or pioneers of a later stage in succession, will be discussed later. Another feature is the occurrence of numerous hemicryptophytes and some geophytes and suffrutices, the former persisting here in the dense shade of the *Erica*. The thin, pale green leaves of these species contrast sharply with those developed in full light: often few and minute, like those of seedlings, they are easily overlooked. However, these leaves are found to be attached to well-developed root or rhizome systems. Most of the hemicryptophytes listed are able to live in tall heath in this fashion.

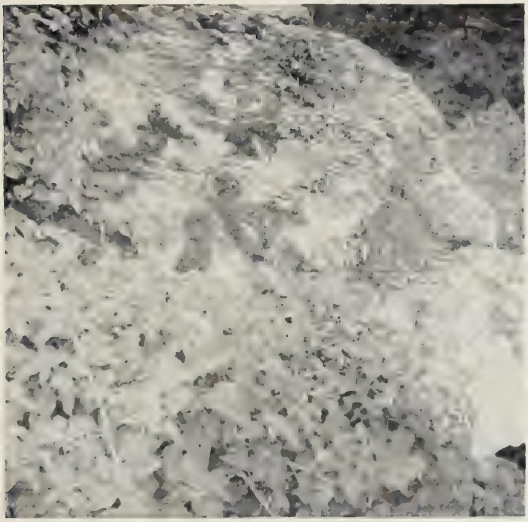
(ii) *Erica demissa—Phylica axillaris*—other spp. heath. The most widespread heath type, at least to 1955, was the *Erica demissa—Phylica axillaris*—other species heath, characterised from the preceding chiefly by the presence of *Phylica axillaris*, but also by *Ursinia anethoides*, *Amphithalea williamsonii* and

KEY to fig. 5

A - Anisotoma mollis
B Berkheya carduoides
C = Cliffortia linearifolia
Ch — Erica chamissonis
⊙ = E. demissa
· d = Seedlings of E. demissa
G = Gerbera viridifolia
Gy = Gymnosporia angularis
H = Helichrysum subglomeratum
Ox = Oxalis punctata
Ⓡ = Restio triticeus
S = Senecio concolor
• Sc - Schoenoxipheum sparteum
△ = Cladonia



TEXT FIG. 5.—Section of 6 in. wide belt transect in undisturbed and apparently mature *Erica demissa* heath. Plan and elevation drawn to scale and semi-naturalistic.



Phot. 9.—Dassie Krantz boulder talus. *Fleurya mitis* straggling over boulders—note creeping habit of some stems. *Plectranthus* sp. and *Adenocline acuta* also present. On rock note contrasted flora of *Cineraria saxifraga, Hypnum cupressiforme* and lichens (*Cladonia, Ramalina, Teloschistis, Parmelia* spp. and small grey encrusting lichen).

Phot. 10.—*Metalasia muricata* heath. An example of dominance by one species.

Plate V

a number of other small shrubs included in the following list, derived from analysis of 25 metre quadrats.

TABLE IX

FLORA OF *ERICA DEMISSA—PHYLICA AXILLARIS* HEATH

Acalypha peduncularis	f–c
Alepidea capensis	c
Alloteropsis semialata	c
Amphithalea williamsonii	o–f
Anthospermum aethiopicum	f–c
Aristida galpinii	f
Athanasia punctata	f
Berkheya carduoides	f
B. decurrens	f
Bobartia burchellii	c
Bo. indica	f
Centella eriantha	f–c
Chaetacanthus setiger	f
Cliffortia repens	o
Clutia heterophylla	c
Cymbopogon marginatus	f
Disparago ericoides	f
Elyonurus argenteus	l.c.
Erica chamissonis	f
E. demissa	c
Eulalia villosa	f
Ficinia sp.	f
Gerbera viridifolia	f
Harpechloa falx	f
Helichrysum anomalum	f
H. appendiculatum	f–c
H. felinum	c
H. nudifolium	c–a
H. subglomeratum	c–a
Hibiscus aethiopicus	o–f
Indigofera stricta	r–o
Metalasia gnaphalodes	l.c.
Phylica axillaris	o–l.d.
Polygala hispida	f
Pteridium aquilinum	o–c
Restio triticeus	f–c
Schoenoxiphium sparteum	c
Senecio othonnaeflorus	c–a
Tephrosia capensis	f
Themeda triandra	a
Tristachya hispida	f
Ursinia anethoides	f–c
Vernonia dregeana	o–f

Rarer plants characteristic of this community are *Helipterum milleflorum*, *Protea cynaroides*, *Psoralea polyphylla* and *Agathosma peglerae*. The structure is more open than that of *E. demissa* heath, the taller heath species do not form a continuous canopy, the height is lower and a larger number of herbs, grasses and small shrubs are present.

(iii) *Metalasia muricata* heath. A single large area of *Metalasia* dominated heath lies between the main *Erica—Phylica* heath and the *Tetraria capillacea* dominated area, as well as a few small patches in the *Erica-Phylica* heath. The type is distinctive, but has not been examined in detail (see phot. 10).

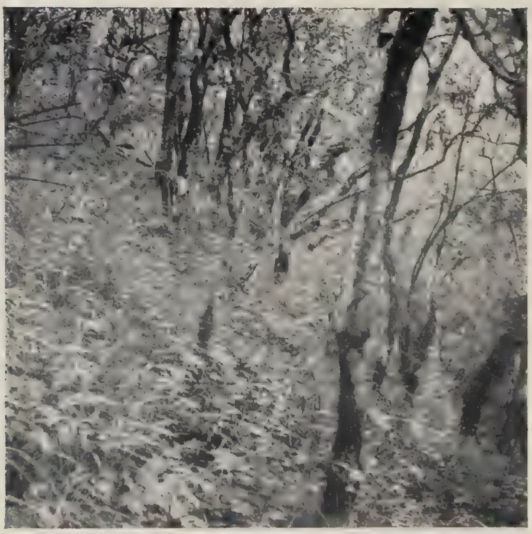
(iv) *Tetraria capillacea*—mixed dwarf shrub heath. This presents a very low-growing, seemingly depauperate open heath type, found mainly on the col between the Howisons Poort and Featherstones Kloof drainage. Its spread down the slope on the Howisons Poort side suggests that exposure to westerly and north-westerly insolation, possibly combined with shallow eroded soils and strong winds, is responsible for its openness. The characteristic plants include a great many chamaephytes.

Table X

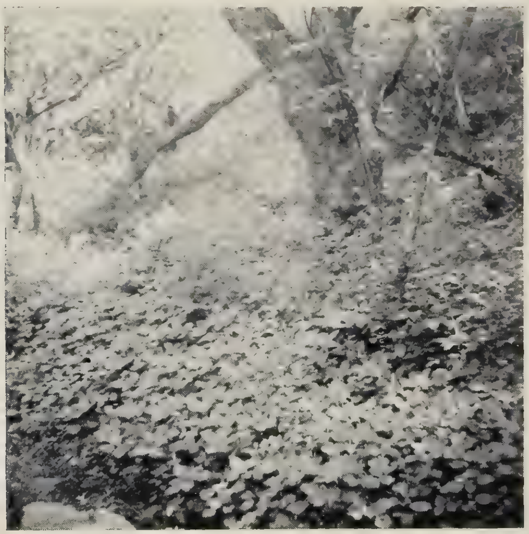
FLORA OF *TETRARIA CAPILLACEA*—MIXED DWARF SHRUB HEATH

Agathosma peglerae	o
Alepidea capensis	f
Amellus strigosus	c
Andropogon appendiculatus	o–f
Anisotoma mollis	o–f
Anthospermum paniculatum	o–f
Argyrolobium spp.	f
Aristea anceps	o
A. pusilla	o–f
Buchnera dura	o
Chaetacanthus setiger	f
Clutia heterophylla	o
Elegia parviflora	l.f.
Eragrostis capensis	f
Erica calycina	v.r.
E. glumaeflora	f
Eriosema salignum	f
Eroeda imbricata	o
Euphorbia striata	o
Ficinia stolonifera	f
Gnidia nodiflora	f
G. sericea	f
Helichrysum squamosum	o
H. subglomeratum	o
Hibiscus aethiopicus	f
Hypericum lalandii	o
Hypoxis obliqua	o
Indigofera fastigiata var. *angustata*	o
I. hilaris	o–f
Leontonyx squarrosus	o
Linum thunbergii	o–f
Leucadendron salignum	o
Lobelia cf. *tomentosa*	c
Osteospermum imbricatum s.sp. *nervatum*	r
Pentaschistis angustifolia	f
Pteronia teretifolia	o
Relhania pungens	f
Restio sejunctus	c
R. triticeus	c
Scabiosa anthemifolia	f
Senecio pinifolius	o
Struthiola argentea	f
Sutera campanulata	c
Tephrosia capensis	c
Tetraria burmannii	v.r.
T. capillacea	l.c.
T. cuspidata	f
Thesium gnideaceum	o
Wahlenbergia capillacea	f

No other heath type has been examined in detail, except the *Festuca—Bobartia* community. Each is characterised by dominance of a single species, mostly the area occupied is small, and probably they owe their origin to disturbance. Thus, pure communities of *Cliffortia linearifolia* arise on cleared firepaths and after fires. *Anthospermum aethiopicum* heath often contains *Hibiscus trionum*, *Selago corymbosa*, *Tephrosia capensis* and *Malvastrum scabrosum*, which tend to behave aggressively, like ruderals, on disturbance of the veld. *Pteridium* is well-known as an invader after disturbance, and while it occurs sporadically in *Erica* heath, it is unlikely to become dominant naturally. *Metalasia* may be an exception, but there is evidence, to be considered in another paper, that burning may have a selective effect on certain species, of which *Metalasia muricata* is one. *Festuca—Bobartia* heath may also be an exception, but here too *Bobartia* is influenced by fires. A *Festuca costata* grassland occurring



Phot. 11.—Woodland below Dassie Krantz, many trees showing coppice form. Ground flora ill-defined, consisting partly of small saplings; canopy irregular. A young type of woodland.



Phot. 12.—More mature woodland, showing greater size of trees. Abundant ground flora of *Plectranthus*. Note lianes.

Plate VI

at altitudes above 6,000 ft. has been described (Acocks, 1953) as *Themeda—Festuca* alpine veld. However, "alpine" is less apposite than "montane" (Adamson, 1938) as few if any of the species are truly alpine in range. Even so, it appears to be below its normal altitudinal range in the present situation. Possibly this grassland type forms a relic of former *Festuca* veld which was dominant on south slopes, steep but with fairly deep soils, often below *Oldenburgia* communities on exposed outcrops higher upslope. Such sites remain in shadow for a large part of the day in winter months and dew lies late. Thus conditions found at higher altitudes may be partly simulated.

The following list includes only the characteristic species. It should be compared with the list given by Acocks (1953), which also includes the supposedly temperate indicators, *Koeleria* and *Poa binata*.

TABLE XI

FLORA OF THE *FESTUCA-BOBARTIA* HEATH

Ajuga ophrydis	r–o	*Gladiolus* sp. indesc. (aff. *tristis*)	o–f
Aspalathus eriophylla	r	*Koeleria capensis*	f
A. setacea	r	*Osteospermum junceum*	o
Bobartia burchellii	a	*Poa binata*	c
Buchenroedera multiflora	l	*Rhyticarpus difformis*	o–f
Dierama pendulum	o	*Scabiosa anthemifolia*	f
Erica cerinthoides	o	*Senecio oxyriaefolius*	o–f
Festuca costata	a	*S. tropaeolifolius*	f
F. scabra	r–o	*Themeda triandra*	c
Gladiolus maculatus	r	*Thesium fruticosum*	o

Clutia affinis heath has little in common with the other heath types. Considered from the point of view of classification, it probably is to be regarded as belonging to a separate alliance. *Polygonum undulatum*, *Tephrosia grandiflora*, *Indigofera stricta*, *Digitaria macroglossa* and *Osteospermum grandidentatum* are characteristic. This type also often contains *Selago corymbosa*, *Tephrosia capensis* and other aggressive species.

The flora of the gravel pit.

At the lower end of the Reserve, near the Howisons Poort road, an old ironstone gravel pit was formerly utilised for roadmetal, before the present National Road was built. When this practice was discontinued is not known, but the pit is unlikely to have been used since declaration of the Reserve, possible for longer. Some gully erosion of the bare subsoil has occurred, but colonisation by the heath is in progress. A list of the species seen in 1950 is given in Table XII.

The two most abundant species were *Restio triticeus* and *Pentaschistis curvifolia*. It therefore seems likely that grass heath with a large number of woody species would become established on bare rock rubble, at an early stage—significant for any theory of plant succession on the Reserve. Ruderal species are relatively scarce, but *Elytropappus*, *Selago*, *Haplocarpha lyrata*, *Rhynchelytrum* and *Pinus* fall into this category. At this stage, the total cover averages not more than 10%, and the cover per square metre varies from nil to 30%.

Table XII

SPECIES GROWING ON EXPOSED SUBSOIL OF GRAVEL PIT

Acalypha peduncularis	r	*Haplocarpha lyrata* (mostly in gully)	l
Agathosma peglerae	o	*Helichrysum anomalum*	o
Anthospermum aethiopicum	o–f	*Hibiscus aethiopicus*	o
Bobartia indica	o	*Lobelia tomentosa*	f
Centella eriantha	o	*Metalasia muricata*	f
Cliffortia linearifolia	f–a	*Moraea setacea*	r
C. repens	o	*Pentaschistis curvifolia*	f–a
Disparago ericoides	f	*Pinus pinaster*	o
Elytropappus rhinocerotis	o	*Relhania pungens*	f
Eragrostis capensis	o–f	*Restio triticeus*	l.a.–d
E. curvula	o	*Rhynchelytrum setifolium*	l
Erica glumaeflora	r	*Selago corymbosa*	f
Eriosema salignum	o	*Senecio concolor*	l
Euphorbia striata	r	*Struthiola parviflora*	o
Gnidia nodiflora	r	*Tephrosia capensis*	o
G. styphelioides	o		

List possibly not complete

(*b*) **Grassland—temperate grassland formation:** (i) Tall tussock grassland subformation; (ii) Low tussock grassland subformation (Martin and Noel, 1960).

Two types of grassland other than the *Festuca—Bobartia* heath may be recognised. Firstly, in the heath-dominated areas, a grass-shrub mosaic or "grass heath" occurs, in which *Cymbopogon marginatus* is very prominent. *Festuca costata* is rare, but *Elyonurus argenteus*, *Themeda triandra*, *Eragrostis curvula*, *Brachiaria arrecta*, *Tristachya hispida*, *Alloteropsis semialata*, *Aristida galpinii* and *Andropogon appendiculatus* are typical.

These areas are often only a few yards in diameter and appear to be natural. It has not been shown however whether the mosaic is stable or undergoes a cyclic succession.

TABLE XIII
FLORA OF TALL TUSSOCK GRASSLAND

Gramineae	
Alloteropsis semialata	c
Andropogon appendiculatus	c
A. filifolius	r
Aristida galpinii	l
Cymbopogon marginatus	l
Elyonurus argenteus	l–c
Eragrostis capensis	f–c
E. curvula	o–f
Eulalia villosa	o–f
Festuca costata	r–o
F. scabra	r
Harpechloa falx	f
Panicum ecklonii	o–f
Pentaschistis angustifolia	f–a
P. thunbergii	f–a
Sporobolus centrifugus	o–f
Themeda triandra	a
Tristachya hispida	o
Others	
Argyrolobium harveianum	o
A. stipulaceum	o
Bobartia burchellii	o–f
B. indica	o–f
Helichrysum appendiculatum	f
Indigofera fastigiata	o
Oxalis bifurca	o
O. imbricata var. *violacea*	l.c.
O. punctata	l.c.
Senecio concolor	c
S. coronatus	o
S. isatideus	o
S. othonnaeflorus	c
Zornia bracteata	r–o

The second type of grassland may not be natural. It is associated with signs of probable disturbance. Just above the main area occur a number of Agaves, a depression which may represent an old earth dam now colonised by *Pteridium*, and, near the centre of the area, an apparent hut site, showing signs of digging. *Setaria flabellata* and *Cynodon dactylon* have become common here, both grasses of disturbed and grazed occupation sites. This is the largest area of more or less pure grassland on the Reserve and the only one where *Setaria flabellata* is abundant. *Eragrostis capensis*, *Digitaria macroglossa*, *Heteropogon contortus*, *Ehrhardta calycina*, *Sporobolus capensis*, *Andropogon appendiculatus* and *Tristachya hispida* are other common grasses. *Tephrosia capensis*, *Gerbera piloselloides* and *Oxalis bifurca* are frequent. The community appears to merge into the mixed dwarf shrub heath and *Pteridium*, which are probably invading it, but the vegetation is evidently fairly stable, as the species list of six analysis circles in this area, quoted by Scott, Norval and Liebenberg, 1933, include most of these species. A few small patches are dominated by *Digitaria macroglossa*, forming a savannah grassland, between 4 and 5 ft. tall at flowering. These may be natural and are a tall tussock type, but as all are close to or included in the disturbed area they are provisionally described with the low tussock grassland.

Table III appears to show that, whereas the tall tussock grassland is pedologically more like the heath, the low tussock type has nitrifying power and pH intermediate between the heath and the woodland, yet low or very low soil organic content, as measured by loss on ignition, while the water content, both shortly after rain had fallen and some weeks later, was lower than that of the tall tussock type (text fig. 8). These data are too few to draw any firm conclusions, but do suggest the likelihood of some pedological site distinction, rather than a purely fortuitous floristic one.

(*c*) **Scrub and forest.** Temperate evergreen forest formation, temperate rainforest subformation: *Olea capensis—Podocarpus latifolius* alliance and temperate rainforest seral transition scrub.

(i) *Structure and composition of scrub and forest.* The scrub and forest on the Nature Reserve are confined mainly to three areas, the largest of which is to the south and east of Dassie Krantz. The second area lies near the lower end of the Reserve in the Featherstones Kloof catchment, and the third and smallest lies overlooking the Howisons Poort road in a small area of perched water table. Small patches also lie along the lower part of the stream draining to the Howisons Poort catchment.

The scrub and forest have many species in common, though some are much more frequent in scrub, for example *Grewia occidentalis* and *Carissa bispinosa;* and others are confined to forest, e.g. *Harpephyllum caffrum.* The difference is mainly one of structure—density and height being the differentiating features. South African ecologists often distinguish "scrub", "bush" and "forest", but the points where "bush" grades into scrub at one end and forest at the other are clearly arbitrary (Phots. 11 and 12).

Scott, Norval and Liebenberg give the following definitions; evergreen scrub—mostly broad-leaved species, gnarled, stunted and liana-bound, and thorny, 8—25 ft. Evergreen bush—mostly broad-leaved, clean-boled trees, 25—40 ft. in height, not gnarled or stunted, with a fair number of lianes. Evergreen forest—mostly broad-leaved trees with heavy canopy, clean-boled, greater than 40 ft. in height, not many lianes or spiny types. Liebenberg (1933) on the other hand, recognised only scrub and bush. "Bush may reach 25—60 ft., has more even canopy, more lianes, fewer armed shrubs, and more mesophytic leaf forms. Dominance does not occur in either scrub or bush canopy."

The distinction is particularly difficult to make in the present instance, as vegetation recognisable as really "high forest" is absent. It is therefore preferable to apply some simple criterion, and in the present instance only two structural types are recognised—"scrub", a low-growing, non-stratified vegetation without marked undergrowth, and "low forest" (or woodland) in which two or three layers are present—herbaceous, shrub layer and canopy—irrespective of species composition, presence of single-stemmed or coppiced growth, frequency of lianes and spiny species, height or any other criteria (though, obviously, there will be some correlations). The one-layered scrub is confined in the main to a small strip near the top of the ridge from just west of Dassie Krantz to the eastern end of the Reserve. Small areas within the woodland also conform to this type. Webb (1959) proposed a new classification of rainforests in Australia, the value of which for South African forest would be worth exploring; further consideration is given to this in the Discussion. According to this classification, the Albany kloof forests would be "simple notophyll vine forests" and "microphyll vine woodlands".

Scott, Norval and Liebenberg (1933, unpub.) made a number of line transects in the two larger areas of woodland and scrub. The transects list all trees and shrubs touching or projecting over the line, but unfortunately, do not give diameter or height of the individual trees. The picture is confused by the fact that few of the transects are confined to a single vegetation type. It is stated that particular transects were "bush merging into forest" and so on. The results for 18 transects are grouped here under the headings "mainly scrub" (7 transects), "mainly bush" (7 transects) and "mainly forest" (4 transects), following the divisions adopted by the authors (Table XIV).

TABLE XIV

LIST OF SPECIES PRESENT IN TRANSECTS OF SCOTT, NORVAL & LIEBENBERG, 1933

Species	Totals mainly "Scrub"	mainly "Bush"	mainly "Forest"	Armed	Scandent	Raunkiaer Leaf Class (C)= compound
Allophylus decipiens ..	2	—	—			(C)mic
Apodytes dimidiata ..	13	32	36			mic
Asparagus sp.	2	2	1	*	*	lepto
Burchellia bubalina ..	11	42	6			meso
Calodendron capensis ..	1	2	—			meso
Canthium ciliatum ..	4	2	—	*		mic
C. mundianum	4	9	—	*		mic
C. ventosum	—	2	1			mic-meso
Carissa bispinosa ..	4	2	2	*		mic
Cassine capensis	1	9	1			meso
Cassinopsis ilicifolia ..	2	7	1	*		mic
Clausena inaequalis ..	5	6	—			(C)mic
Clutia affinis	—	3	—			n-mic
Cotyledon velutina ..	8	—	—			meso
Curtisia dentata ..	6	34	18			meso
Cussonia spicata ..	1	15	6			(C)meso
Dovyalis rhamnoides ..	3	7	9	*		mic
Euclea macrophylla ..	7	—	—			mic-meso
E. ? lanceolata	17	—	—			mic
Eugenia zeyheri	—	3	28			mic
Fagara capensis ..	5	1	1	*		(C)mic
Gardenia neuberia ..	14	1	—	?*	?*	mic
G. thunbergii	—	14	—	?*		meso
Grewia occidentalis ..	14	1	—			mic
"*Gymnosporia buxifolia*"	74	—	—	*		mic-meso

Species	Totals			Armed	Scandent	Raunkiaer Leaf Class (C)= compound
	mainly "Scrub"	mainly "Bush"	mainly "Forest"			
Halleria lucida	6	15	1			meso
Harpephyllum caffrum . .	—	—	6			(C)meso
Heteromorpha arborescens	5	1	—			(C)mic
Hippobromus pauciflora	6	12	—			(C)mic
Ilex mitis	—	1	—			meso
Maerua racemulosa . .	6	—	22			mic
Maytenus nemorosus . .	36	40	21	*		meso
M. peduncularis . .	1	5	13			meso
Ochna arborea	—	2	6			mic
Olea capensis s.sp. *capensis*	3	3	15			meso
Pavetta lanceolata . .	—	—	4			mic-meso
Pittosporum viridiflorum	—	2	5			meso
Pleomele hookeriana . .	—	1	—			macro
Plumbago capensis . .	1	—	—		?	mic
Podocarpus falcatus . .	—	—	1			n-mic
P. latifolius	1	1	7			mic
Pterocelastrus tricuspidatus	—	—	5			mic-meso
Rapanea melanophloeos . .	22	45	6			meso
Rhoicissus capensis . .	1	—	—		*	meso
R. cuneifolia	6	61	5		*	(C)mic
Rhus legati	4	12	9			(C)meso
Royena lucida	—	24	6			mic
R. lycioides	13	—	—			mic
R. pubescens	2	—	—			mic
R. villosa	—	—	1		*	meso
Scolopia mundii . .	4	1	1	*		meso
Scutia indica	69	45	9	*	*	mic
Secamone alpini . .	3	3	3		*	mic
Senecio deltoideus . .	5	—	—		*	mic
Sideroxylon inerme . .	6	—	—			meso
Trimeria trinervis . .	—	6	2			mic-meso
Vepris undulata	2	1	—			(C)meso
Unidentified (varia) . .	1	1	2			—
Total	403	420	259			
Total length of transect (100 ft. units) . .	700 ft.	700 ft.	400 ft.			
No. of individuals/unit length	0·58	0·60	0·65			
No. of species recorded	43	40	35			
No. of armed individuals	221	116	46			
Percentage of armed individuals	54·8	27·6	17·8			
No. of scandent individuals	86	56	19			
Percentage of scandent individuals	21·5	13·3	7·4			

It is clear that, whereas the distinction between scrub and the others is quite recognisable, many of the species differences between "bush" and "forest" appear to be quite fortuitous; possibly a more selective placing of the transects would have brought out more real differences between the types. Certain trends are apparent, however; the greater abundance of *Podocarpus* spp., *Apodytes* and *Olea*, and the reduced abundance of *Scutia* in forest and the replacement of "*Gymnosporia buxifolia*" by *Maytenus nemorosus* and *M. peduncularis*. *Cotyledon velutina*, *Plumbago capensis* and *Euclea lanceolata* appear to be confined to scrub. The decline of spiny species in forest is quite clear, but the decline in scandent species in both bush and forest is not altogether consistent, either with Liebenberg's definition or my own experience, though Scott, Norval and Liebenberg include a decline in the numbers of lianes in their definition of forest. The data may be atypical in this respect. Certain common lianoid species, such as *Clematis brachiata* ,have been missed, and the abundance of *Rhoicissus* spp. and climbing *Senecio* spp. seems remarkably low.

With the above criticism kept in mind, the data may be compared with those quoted by Seagrief (1950), and by Story (1951) for Albany, and by Story (1953) for scrub and forest types at Keiskamma Hoek. The percentage of spiny species in the Nature Reserve scrub appears fully as great as that quoted for the most arid and stunted scrub type of the Keiskamma Hoek basin (Fort Cox scrub), despite the absence from the list of several spiny shrubs, e.g. *Acacia karroo*, *Azima tetracantha* (both present in the scrub of the Reserve, though uncommon). Certain other characteristic species of the Fort Cox scrub are absent or rare, e.g. *Jasminum multipartitum*, *Randia rudis* and *Olea africana*. It is at first surprising that communities in climatically distinct conditions show such close floristic and physiognomic resemblances, Fort Cox scrub (climatic data of Story, 1953) being drier, with a more definite summer rainfall, less liable to mists and receiving higher temperatures than Grahamstown, (climatic data of Dyer, 1937), but this ubiquity or wide climatic tolerance appears to be a characteristic of many scrub species.

The aggregate "low forest" vegetation may be compared with Story's "Zanyokwe bush" and "Dry" and "Moist" forests as regards degree of spininess. In regard to species composition, they compare most closely with the moist forest. Thus, *Apodytes dimidiata*, *Curtisia dentata*, *Burchellia bubalina*, *Calodendron capensis*, *Halleria lucida*, *Ilex mitis*, *Ochna arborea* and *Podocarpus* spp. all appear to be most typical of moist forest at Keiskamma Hoek, though not entirely absent from the drier types.

Undergrowth in scrub is absent or confined to open spaces between the shrubs. *Setaria lindenbergiana*, *Plectranthus thunbergii*, *Crassula cultrata*, *Melica racemosa*, *Sporobolus pyramidalis*, *Petamenes aethiopicus*, *Pandiaka* *leptostachya*, *Silene capensis*, *Lepidium africanum*, *Pellaea viridis* and *Delosperma* spp. are characteristic.

Once a canopy is formed, a typical forest undergrowth, quite species-rich though scattered, develops, consisting of the following:—

TABLE XV

FLORA OF FOREST UNDERGROWTH

Shrubs (3—15 ft.) and small climbers	
Allophylus decipiens	o
Asparagus asparagoides	o
A. macowani	o–f
A. plumosus	o–f
Burchellia bubalina	o
Canthium ciliatum	o–f
C. mundianum	o
Carissa bispinosa	o
Cassine tetragona	r
Cassinopsis ilicifolia	o–f
Dovyalis rhamnoides	o–f
Gardenia neuberia	r
Halleria lucida	o–f
Hippobromus pauciflora	f
Maerua racemulosa	o–f
Ochna arborea	o
Osyridicarpos capensis	o–f
Pavetta lanceolata	o
Pavonia meyeri	r
Pleomele hookeriana	l.c.
Rhoiacarpos capensis	o–f
Rhoicissus rhomboidea	f
Royena pubescens	o–f
R. villosa	r
Herbs	
Acalypha ecklonii	r
Adenocline acuta	c–l.a.
Argyrolobium tomentosum	o
Australina acuminata	r
Brownleea coerulea	o
Cardamine africana	o
Ceratiosicyos ecklonii (climber)	o
Cyperus albostriatus	f
Dietes vegeta	l
Euphorbia kraussiana	o–f
Galopina circaeoides	f–c
Habenaria arenaria	l
Herbs (cont.)	
Pe. reflexa (epiphyte)	f
Plectranthus ciliatus	c–a
Pl. hirtus	o–f
Pl. laxiflorus	o–f
Pl. thunbergii	o
Senecio quinquelobus (climber)	r
Sida triloba	o
Solanum nigrum	o
Stenoglottis fimbriata	o
Stipa dregeana	r
Streptocarpus rexii	f–c
Vicia sativa	r
Zantedeschia aethiopica	r
Pteridophyta	
Asplenium aethiopicum	c
A. erectum	o–f
A. lunulatum	o–f
A. rutaefolium	c
A. splendens	o–f
Blechnum capense	o
B. punctulatum	l.c.
Dryopteris inaequalis	o
D. pentheri	o–f
Hypolepis sparsisora	r
Lycopodium gnidioides	r
Pellaea viridis var. *macrophylla*	f
Pleopeltis lanceolata (epiphyte)	o
Polystichum adiantiforme	l.c.
Pteris dentata	o
Bryophyta	
Aerobryopsis capensis	
Eulejeunia isomorpha	
Fissidens glaucescens	
F. cf. pycnophyllus (sterile)	

H. falcicornis	r	*Leptodon smithii*
Hypoëstes aristata	l.c.	*Lophocolea bidentata*
H. verticillaris	c–l.a.	*Macromitrium tenue*
Lapeyrousia cruenta	f	*Madotheca capensis*
Leonotis dubia	r	*Metzgeria* sp.
Lithospermum officinale	r	*Neckera valentiniana*
Myosotis intermedia	l.f.	*Papillaria africana*
Oplismenus hirtellus	f	*Pleuropus sericeus*
Panicum deustum	f	*Porothamnium natalense*
P. maximum	o	*Radula capensis*
Peperomia retusa (epiphyte)	f	*Rhodobryum roseum*

Through this woodland a number of permanent tracks have been made. Since 1954, some of them have been bordered and partially paved with rocks from the forest floor. The influence of this added source of disturbance has not been investigated. The following list refers to the species known to occur along tracks prior to 1954.

TABLE XVI

FLORA OF BUSH TRACKS (NEAR DASSIE KRANTZ)

Abutilon mollissimum
*Acalypha ecklonii**
Adenocline acuta
Berkheya carduoides
Carpobrotus edulis (R)
Conyza pinnata
C. ulmifolia
Cotula heterocarpa (R)
Cynodon dactylon (R)
Danthonia curva
Eragrostis sp.
Euphorbia kraussiana
Galopina circaeoides
Helichrysum anomalum
H. foetidum
Helictotrichum turgidulum
Hypoëstes verticillaris
Hypoxis obliqua
*Lapeyrousia cruenta**
*Leidesia obtusa**
Lepidium africanum (R)
Panicum maximum
Pelargonium alchemilloides (R)
*Plectranthus ciliatus**
P. thunbergii
Poa aff. *trivailis*
Ranunculus multifidus
Senecio pterophorus (R)
Silene capensis
Solanum nigrum (R)
Sporobolus capensis (R)
S. fourcadei
*Streptocarpus rexii**
*Wahlenbergia oppositifolia**
W. procumbens (R)
W. stellarioides (R)
Vulpia bromoides (R)

* Occurring in denser shade.
(R) — Ruderal and semi-ruderal species characteristic of disturbed ground.

Several of the species are natural constituents of forest undergrowth (e.g. *Streptocarpus*, *Lapeyrousia*, *Plectranthus* etc.), but a noticeable feature is the occurrence of many species otherwise quite absent or unimportant in the composition of forest undergrowth, including a number of grasses. These

PHOT. 13.—Clearing in woodland being colonised by *Canthium mundianum.*

PHOT. 14.—Effect of cattle grazing under woodland canopy—grazed out area under "Gymnosporia buxifolia". Ground flora includes only *Solanum aculeatum,* scattered *Hypoëstes verticillaris* and occasional seedlings of tree, *Fagara capensis.*

PLATE VII

are mostly in the more highly lit (e.g. scrub) areas; only *Panicum* spp. penetrate shade. The remainder are mostly pioneers of lithosere, e.g. *Hypoëstes*, *Helichrysum foetidum*, *Adenocline acuta*. *Acalypha ecklonii* and *Wahlenbergia oppositifolia* seem to form a special component of forest paths, being found only adjacent to these limited areas.

The ruderal component, likewise, does not penetrate into deep shade, where the paths are almost devoid of flora.

The bryophytic flora was not completely recorded, but includes *Hypnum cupressiforme*, *Pleuropus sericeus*, *Mnium rostratum* and *Tortula pilifera*, *Mnium* being typical of moist conditions.

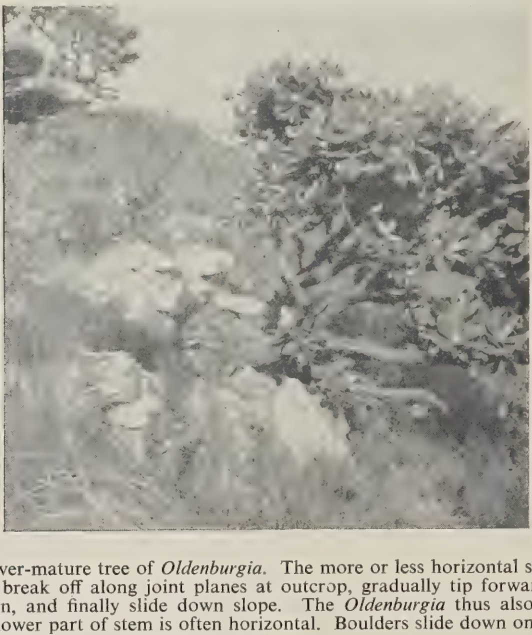
(ii) *Small clearings in the woodland.* These glades are a very characteristic feature of level ground within the forested area. They vary from about 5 to 30 yards in width, are linked together by a series of paths, and are places where cattle congregate. They are grass-clad, with species such as *Poa c.f. trivialis*, *Sporobolus capensis*, *Eragrostis plana* and *Cynodon dactylon* making up most of the cover. The typical clearing consists of a turf of these grasses, in which many ruderals and other species occur. Saplings of forest species are common at the edges, especially *Rapanea*, *Canthium* sp., *Burchellia bubalina*, *Eugenia* and *Royena pallens*. These are mostly natural precursors of scrub growth, (phot. 13), but as long as cattle continue to utilise the clearings (and it is noticeable how they do seem to choose particular spots where they congregate year after year) complete colonisation by trees is not likely. This shows that even with low average grazing intensity, heavy local overgrazing can still occur.

Locally, completely bare areas may develop (phot. 15), usually showing deep hoofmarks and dung. They are probably due to a combination of several factors, mostly drought and cattle trampling, and they are colonised by ruderals and xerophytic mosses. The three mosses *Triquetrella tristichia*, *Tortula pilifera* and *Hyophila zeyheri* form mats between grasses and so act as pioneers in a subsere, as is seen from the ease with which seedlings of forest species develop.

These clearings have existed for many years, and their origin is not easy to trace. Possibly they are the result of gradual enclosure of small areas of grassland or former heath by scrub. In favour of this view is the seeming youthfulness of most of the surrounding forest, while a soil profile dug in one of these clearings contained hard clay at c. 1 ft. depth in a reddish sandy soil. This is quite distinct from the normal profile of forest, and indicates considerable, and longstanding differences in pedogenesis in the level clearings and the wooded slopes. On the other hand, felling or natural death of trees has clearly been involved too, for in some clearings the decayed remains of one or more prostrate trunks may be seen.

In the woodland with cover still intact, cattle sometimes make their way and cause a removal of undergrowth beneath the canopy (phot. 14). Small

Phot. 15.—Effect of cattle grazing in woodland clearing. Bare soil with numerous annual plants and xeric mosses.



Phot. 16.—Over-mature tree of *Oldenburgia*. The more or less horizontal strata of Witteberg break off along joint planes at outcrop, gradually tip forward as boulders loosen, and finally slide down slope. The *Oldenburgia* thus also tips forward. The lower part of stem is often horizontal. Boulders slide down on it from above and tree finally overbalances and falls.

Plate VIII

shrubs and the natural growth of *Plectranthus* and *Hypoëstes* disappear under grazing, and are replaced by herbaceous lianes, *Panicum deustum* and a few other shade-enduring grasses. *Panicum deustum* grows in quite deep shade and seems an indicator of grazing in scrub and forest. If now a large tree were to die and fall over, the space so opened would be colonised by grasses such as *Cynodon*, and ruderals. While one may visualise clearings originating in this way, a soil profile more reminiscent of forest would be expected.

TABLE XVII

FLORA OF THE BUSH CLEARINGS

Abutilon mollissimum	o
Achyranthes aspera	o–f
Alchemilla capensis	o
Anagallis arvensis	o
Anthospermum lanceolatum	o–f
Aristea ecklonii	o
Berkheya carduoides	l.a.
Briza maxima	r–o
Bulbostylis humilis	o
Burchellia bubalina (young)	r
Canthium sp.	l.c.
Carpobrotus edulis	l.c.
Centella eriantha	l.a.
Clematis brachiata	o
Cliffortia linearifolia	o
Clutia affinis	l.a.
Crassula campestris	o
C. lineolata	l.a.
Cynodon dactylon	a
Danthonia curva	r
Dietes vegeta	r–o
Eragrostis capensis	c
E. curvula	c
E. obtusa	o
Euphorbia kraussiana	o–f
Falkia repens	o–f
Galenia pubescens	l.c.
Galopina circaeoides	f
Haplocarpha lyrata	f
Helichrysum cymosum	f
H. foetidum	c
H. nudifolium	f
H. odoratissimum	l.a.
H. petiolatum	o
Helictotrichum turgidulum	o–f
Nidorella auriculata	l.c.
Oxalis bifurca	o–f
Pandiaka leptostachya	f
Panicum deustum	o
P. maximum	o
Pelargonium alchemilloides	f
Plectranthus ciliatus	o
Pl. thunbergii	o
Poa aff. *trivialis*	o
Polycarena cf. *bracteata*	o
Polygonum undulatum	l
Ranunculus multifidus	l.a.
Rapanea melanophloeos	o
Rhoicissus dimidiata	o
Rhus legati	o
Rhynchosia caribaea	f
Royena pubescens	o
Rubus pinnatus	f–c
Schoenoxiphium sparteum	f
Selago corymbosa	f–a
Senecio concolor	f–a
S. deltoideus	o
S. pterophorus	l.a.
Setaria flabellata	f
Sida triloba	r–o
Sisymbrium capense	l
Solanum sodomaeum	o
Sporobolus capensis	c
Sutera cordata	f
Teucrium capense	f
Tolpis capensis	o–f
Trifolium burchellianum	l.a.
Venidium decurrens	l.c.
Vulpia bromoides	o
Wahlenbergia procumbens	f
Pteridophyta	

FLORA OF THE BUSH CLEARINGS *cont.*

Hermannia hyssopifolia	o	*Asplenium platyneuron*	r
Hibiscus trionum	o	*Mohria caffrorum*	f
Hypochaeris radicata	c	*Pellaea viridis*	f
Hypoëstes verticillaris	l.c.	Bryophyta and Lichens	
Hypoxis obliqua	f	*Bryum truncorum*	
Kyllinga erecta	o–f	*Campylopus* cf. *introflexus*	
Leonotis leonurus	o	*Hyophila zeyheri*	
Lepidium africanum	f	*Hypnum cupressiforme*	
Lobelia erinus	o	*Tortula pilifera*	
L. scabra	o–f	*Triquetrella tristichia*	
Lycium ferocissimum	r	*Cladonia floerkeana*	

(iii) *Ecotones between the woodland and other communities.* Tangles of *Rubus pinnatus*, *Helichrysum petiolatum* and others often occur at the edge of forest. However, the margin between quite tall woodland, 25 to 40 ft. high, and such tangles is often sharp, suggesting possibly some factor which has arrested forest advance, or removed scrub elements from the margin. Such sharp ecotones may be the result of fire, or small scale timber-getting, e.g. for firewood or fence posts. Ring-barking by small rodents e.g. Vlei rats (*Otomys* spp.) has also been advanced as a reason for sharp forest-heath or grassland ecotones, but I have not observed any obvious cases of this in the Reserve, although Vlei rats are common.

Round the edges of the woodland small consocies of pioneer forest species clearly show that the woodland is capable of invading other communities if undisturbed. The two chief consocies are of *Rapanea melanophloeos* and *Canthium mundianum* (phot. 13), while *Tarchonanthus camphoratus* sometimes occurs as solitary trees on the edge of tangles. Solitary small trees of *Cussonia spicata* and *Podocarpus latifolius* may also occur, and small plants of *Burchellia*, *Halleria* and species of *Rhus* have already been shown to be occasional in undisturbed heath. Thus there is evidence that forest and scrub species are able at the present day to invade heath and grassland. Photographs of the eastern slopes of Dassie Krantz taken during the 1930's and in 1956 show the advance of the forest margin in this period. Cronwright Schreiner (1930) quotes the lessee of the grazing rights who in 1925 considered that the forest on Dassie Krantz had advanced since his youth, despite the making of paths. Thus the spread of forest is slow but of long standing, and there is no evidence that enclosure of the Reserve alone has caused this.

(5) Hygrophilous Communities.

Owing to the uneven topography, varying in slope and aspect, and in influence of the rock (often resulting in impeded drainage and perched water tables) there are many places where small areas of particularly favourable environment occur in heath or grassland. These are usually marked by a greater luxuriance (height and density) of the flora, and by the presence of some of the following species.

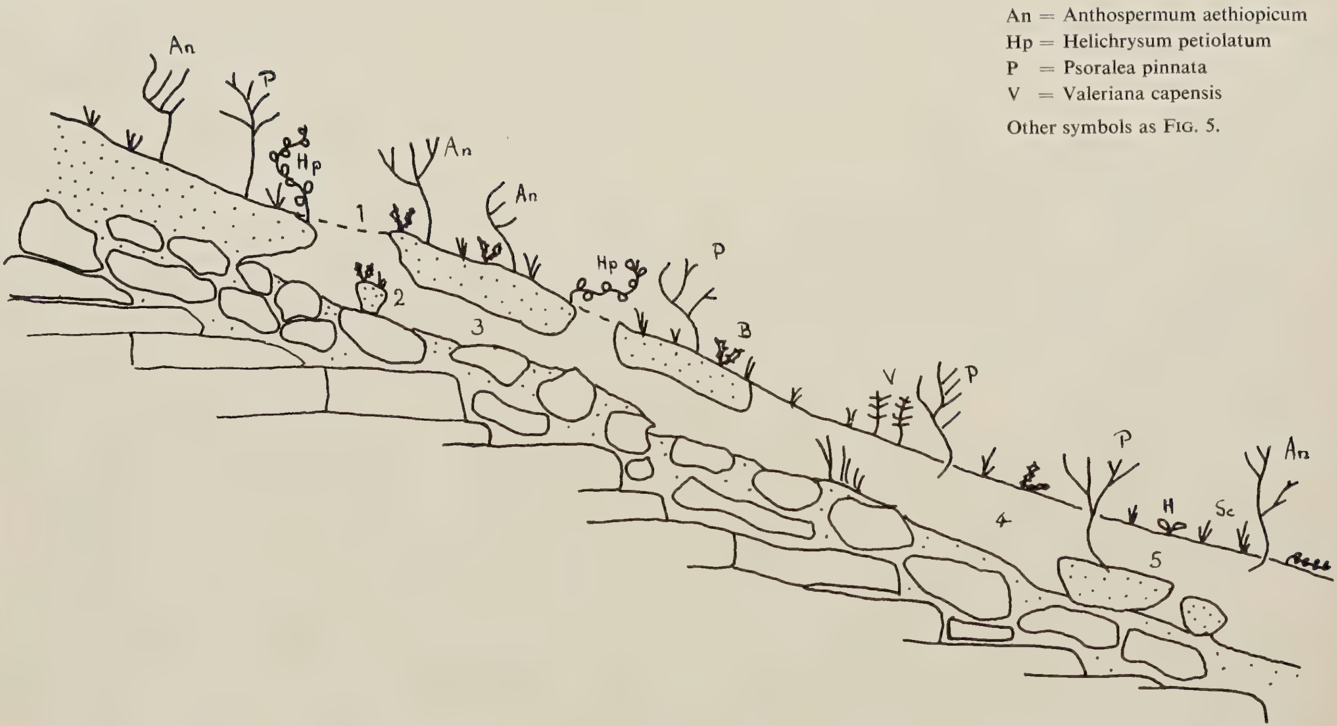
Table XVIII

SPECIES CHARACTERISTIC OF AREAS OF MORE FAVOURABLE WATER BALANCE

Anthospermum aethiopicum
A. lanceolatum
Athanasia punctata
Bulbine altissima
Burchellia bubalina
Chironia melampyrifolia
Cineraria lobata
Clutia affinis
C. hirsuta
Cymbopogon marginatus
Cyphia heterophylla
Diclis reptans
Digitaria diagonalis
Euclea lanceolata
E. undulata
Eucomis undulata
Geranium ornithopodum
"*Gymnosporia angularis*"
Halleria lucida
Hebenstreitia dentata
Hermannia hyssopifolia
H. velutina
Helichrysum petiolatum
Leonotis leonurus
Lobelia hirsuta
Malvastrum scabrosum
Myrsine africana
Nidorella auriculata
Osteospermum grandidentatum
O. herbaceum
Printzia pyrifolia
Psoralea pinnata
P. spicata
Pteridium aquilinum
Rapanea melanophloeos
Rhus dentata
R. eckloniana
R. fastigiata
R. pyroides
Rhynchosia caribaea
Rhynchosia sp.
Rubus pinnatus
Schistostephium flabelliforme
Sutera cordata
S. mollis
Tarchonanthus camphoratus
Tephrosia grandiflora
Valeriana capensis
Venidium decurrens

These species cannot be considered to form a distinct community, as usually only some will be present, but the occurrence of a large number of them is a clear indication of conditions suitable for forest growth.

The species listed above are, in general, characteristic of well-shaded hollows of southerly aspect, and analyses of soils show that the water content is higher than in adjacent heath and grassland. However, there are small areas where distinctly wet conditions arise. Gullies are small channels, usually not more than 2 to 3 ft. deep, cut into the mineral soil, usually to the subsoil or bedrock. These have generally either cut back into more mature vegetation from below, or have resulted from erosion starting from springs higher up. They frequently have steep earth banks with relatively mature soil profile, and have thus arisen by the destruction and modification of the former vegetation. Rafts or islands of soil carried down with vegetation *in situ* may often be seen lying in their

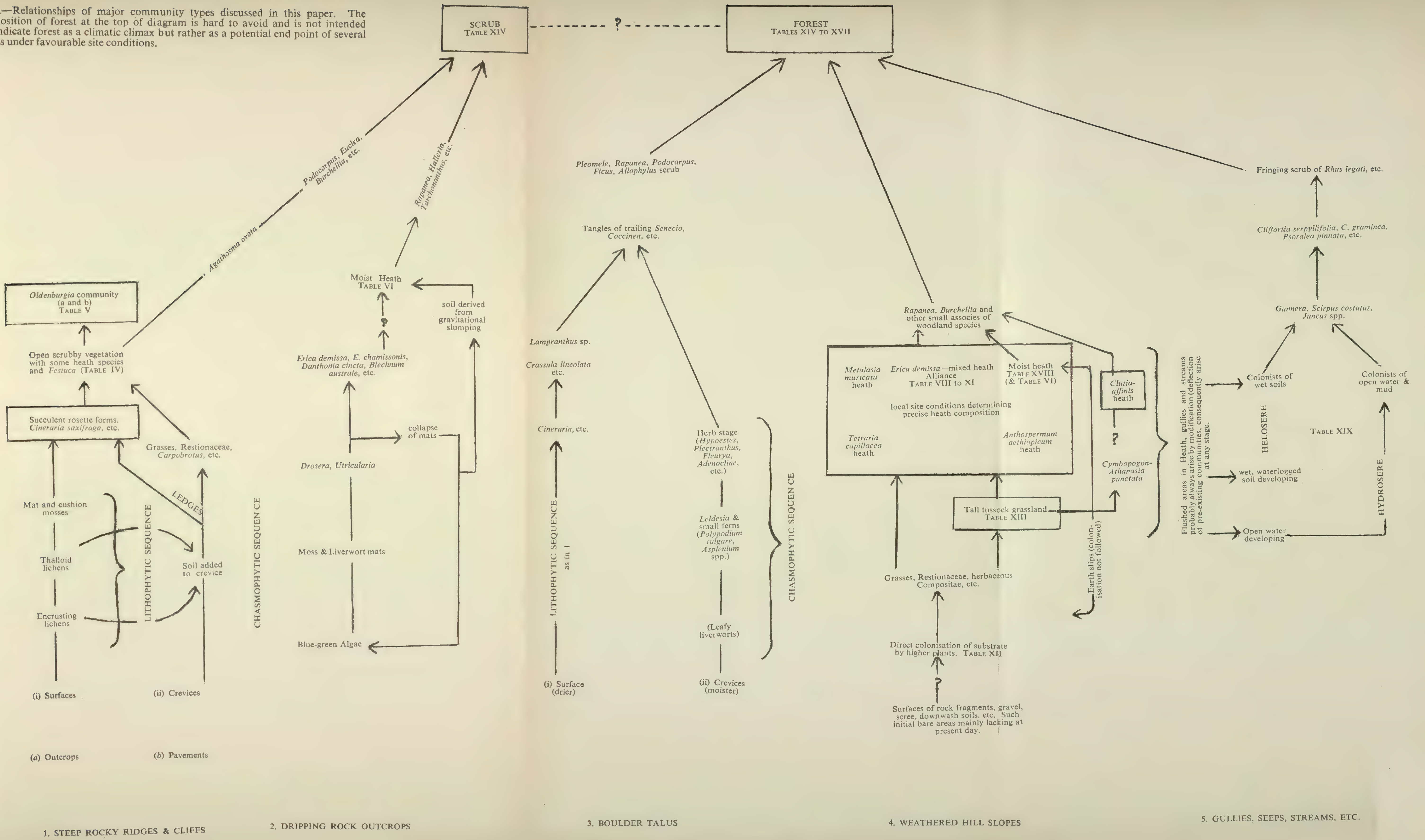


An = Anthospermum aethiopicum
Hp = Helichrysum petiolatum
P = Psoralea pinnata
V = Valeriana capensis

Other symbols as FIG. 5.

TEXT FIG. 6.—Diagram showing cutting back of gully by tunnelling and concentration of hygrophytic shrubs and herbs along gully margin: (1) Sink-hole due to collapse of soil column into tunnel; (2) Vegetation *in situ* on soil column; (3) Tunnel with earth bridge; (4) Open part of gully; (5) Earth rafts in floor of gully with *in situ* vegetation.

TEXT FIG. 7.—Relationships of major community types discussed in this paper. The disposition of forest at the top of diagram is hard to avoid and is not intended to indicate forest as a climatic climax but rather as a potential end point of several seres under favourable site conditions.


SCRUB
TABLE XIV
?
FOREST
TABLES XIV TO XVII
Podocarpus, Euclea, Burchellia, etc.
Agathosma ovata
Rapanea, Halleria, Tarchonanthus, etc.
Pleomele, Rapanea, Podocarpus, Ficus, Allophylus scrub
Fringing scrub of Rhus legati, etc.
Oldenburgia community (a and b) TABLE V
Open scrubby vegetation with some heath species and Festuca (TABLE IV)
Succulent rosette forms, Cineraria saxifraga, etc.
Grasses, Restionaceae, Carpobrotus, etc.
LEDGES
Mat and cushion mosses
Thalloid lichens
Encrusting lichens
LITHOPHYTIC SEQUENCE
Soil added to crevice
CHASMOPHYTIC SEQUENCE
(i) Surfaces
(ii) Crevices
(a) Outcrops
(b) Pavements
1. STEEP ROCKY RIDGES & CLIFFS
Moist Heath TABLE VI
?
Erica demissa, E. chamissonis, Danthonia cincta, Blechnum australe, etc.
soil derived from gravitational slumping
collapse of mats
Drosera, Utricularia
Moss & Liverwort mats
Blue-green Algae
2. DRIPPING ROCK OUTCROPS
Tangles of trailing Senecio, Coccinea, etc.
Lampranthus sp.
Crassula lineolata etc.
Cineraria, etc.
LITHOPHYTIC SEQUENCE as in 1
(i) Surface (drier)
Herb stage (Hypoestes, Plectranthus, Fleurya, Adenocline, etc.)
Leidesia & small ferns (Polypodium vulgare, Asplenium spp.)
(Leafy liverworts)
(ii) Crevices (moister)
CHASMOPHYTIC SEQUENCE
3. BOULDER TALUS
Rapanea, Burchellia and other small associes of woodland species
Metalasia muricata heath
Erica demissa—mixed heath Alliance TABLE VIII to XI
Moist heath TABLE XVIII (& TABLE VI)
Clutia-affinis heath
local site conditions determining precise heath composition
Tetraria capillacea heath
Anthospermum aethiopicum heath
?
Cymbopogon-Athanasia punctata
Tall tussock grassland TABLE XIII
Earth slips (colonisation not followed)
Grasses, Restionaceae, herbaceous Compositae, etc.
Direct colonisation of substrate by higher plants. TABLE XII
?
Surfaces of rock fragments, gravel, scree, downwash soils, etc. Such initial bare areas mainly lacking at present day.
4. WEATHERED HILL SLOPES
Cliffortia serpyllifolia, C. graminea, Psoralea pinnata, etc.
Gunnera, Scirpus costatus, Juncus spp.
Colonists of wet soils
Colonists of open water & mud
Flushed areas in Heath, gullies and streams probably always arise by modification (deflection of pre-existing communities, consequently arise at any stage.
HELOSERE
TABLE XIX
wet, waterlogged soil developing
Open water developing
HYDROSERE
5. GULLIES, SEEPS, STREAMS, ETC.

beds after heavy rains, and observation over a period leaves no doubt that the heads of some of the streams are migrating uphill. Often their upper reaches are marked by the occurrence of earth bridges, the stream running by means of a tunnel for distances of few to many yards. In some such cases, the presence of a stream is only shown by an occasional hole where the roof has caved in. Such phenomena all suggest a fairly recent origin for the gullies (text fig. 6). However, along their courses succession seems often to have been accelerated, as, presumably due to the increased water content of the soil and periodic presence of flowing water, shrub growth commences along their banks. In the upper part of the gullies the stream beds themselves are generally bare, though the banks may be marked by a growth of more hygrophilous shrubs and herbs (Table XVIII). In the lower parts of the course, communities of marsh plants have developed in the small accumulations of alluvial deposits. and a new succession via hygrophilous shrubs to forest seems to have commenced. These stages may be held to represent a helosere or hydrosere, but from the point of view of origin they appear to be superimposed on the general development.

Where flushing by underground water is involved (cases 2*a*, 2*b* and 5, p. 9), the water table is also permanently closer to the surface than average, and the soil often moist to waterlogged for longer than average periods after heavy rains. It is in these areas that earthslips occur if the slope is steep enough. In such places, indicator species from Table XVIII will be present. *Valeriana capensis* and *Athanasia punctata* are particularly indicative. *Carex zuluensis*, *Pelargonium radula* and *P. graveolens*, *Kniphofia uvaria* and *Pennisetum macrourum* may be present. The luxuriance of the vegetation increases. *Erica chamissonis*, though by no means confined to such moist heath, is often common or dominant in well-flushed areas.

In any of these cases a more luxuriant vegetation arises from a less luxuriant type as degradation proceeds. In each case this is due to a local increase in soil moisture content and the vegetation change is scarcely to be regarded as part of a helosere, but as a xerosere deflected from its course by locally superimposed soil conditions.

(6) Community Types of Aquatic and Semi-Aquatic Conditions.

There are two semipermanent streams at the lower end of the Reserve where the drainage lines begin to converge, one joining the Howisons Poort, the other the Featherstones Kloof catchment. The following species are present, groupings dominated by single species over small areas being frequent, as indicated, but the status of such communities has not been investigated.

TABLE XIX

OPEN WATER AND MUD

Anagallis huttonii	
Asterochaete glomerata	
Eleocharis limosa	
Grammatotheca bergiana	
Gunnera perpensa	
Ilysanthes gratioloides	
Juncus capensis	
J. lomatophyllus	l.d.
J. oxycarpus	
Laurentia arabidea	
Limosella aquatica	
Lobelia erinus	
Lysimachia nutans	
Lythrum hyssopifolia	
Phragmites communis	l.d.
Polygonum setulosum	
Scirpus costatus	l.d.
S. ludwigii	

STREAM BANKS AND WET SOILS

Afrachneria ampla	
Carex zuluensis	
Cliffortia graminea	l.d.
C. serpyllifolia	l.d.
Conyza ivaefolia	
Co. pinnata	
Geranium caffrum	
Gnaphalium purpureum	
Gnidia oppositifolia	l.d.
Hermannia hyssopifolia	l.d.
Mariscus congestus	
M. owanii	
M. riparius	
Mentha aquatica	
Nidorella auriculata	
Nidorella undulata	
Ornithogalum comptum	
Pelargonium graveolens	
Pennisetum macrourum	l.d.
Plectranthus laxiflorus	l.d.
Psoralea oligophylla	
P. pinnata	
Pulicaria scabra	
Pycreus lanceus	
Senecio purpureus	
S. rigidus	
Setaria sphacelata	
Valeriana capensis	
Venidium decurrens	
Zantedeschia aethiopica	l.d.

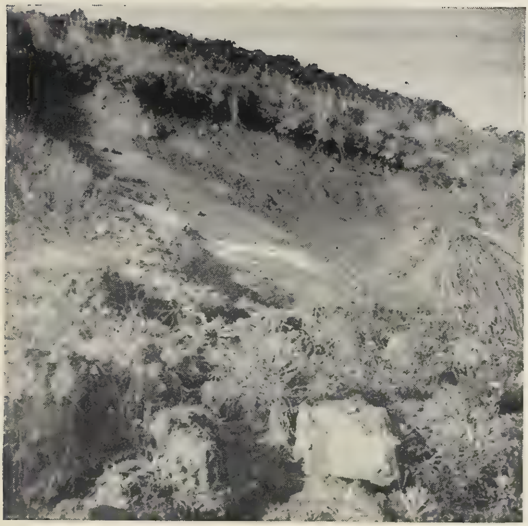
It is doubtful if these streams are truly perennial, except in periods of abnormally wet years. In a dry year they are reduced to a series of muddy stagnant puddles.

DISCUSSION

1. Succession.

In the light of the considerations on pages 9 and 10, the following generalisations may be made and are put diagrammatically in Text fig. 7. In this diagram, the inferred successional status of each of the various community types is indicated.

(*a*) On steep slopes erosion and development proceed concurrently; thus the *Oldenburgia arbuscula* community on rock outcrops is unstable as the result of the collapse of over-mature trees, rock falls and the slumping of soil masses to lower level. Earlier stages of succession are mixed with later ones, and *Oldenburgia* represents a physiographic climax in a state of cyclical fluctua-



PHOT. 17.—Earth slip in heath. This is a site receiving water flowing over bedrock. In wet conditions soil may become temporarily saturated and slide down slope. Forest in background due to perched water table.

PLATE IX

tion (phot. 16). An expression of the same principle is seen in the cyclical development of heath in moss mats on ledges of wet rock, described on pp. 15 and 16. A rather different expression of the same principle is seen in the way that erosion, in cutting back the heads of gullies, establishes locally drier and moister areas in formerly more uniform ones.

(*b*) The land surface is an old one, which has been eroded into its present form very slowly. Early stages of prisere are therefore few in number, cover small areas and are disjunct with each other. Most succession seen is at least in part secondary. The ability of shrubs and grasses to colonise bare areas such as screes and rock rubble shows that lichen and moss stages of the hypothetical prisere are often bypassed. The colonisation of the gravel pit by *Restio*, *Pentaschistis* and shrubs is further evidence of this.

(*c*) A "poly-climax" viewpoint is adopted. The importance of differences in topography and of microtopography is strongly emphasized. Succession has taken different courses in areas of different initial topography, while the concept of the cosere—a patchwork of seres of different origin, proceeding and converging towards a relatively small number of climax types, is the most readily applicable to the mosaic of successional stages seen in each topographical area. Such mosaics occur often in a very small area and may develop at different rates; thus on Witteberg "pavements" on the top of the ridges, with a microtopography of flat rock surfaces and crevices, a long-persisting, slowly developing lichen stage occurs on the surface of the slabs, while a much more rapidly developing grass-heath occurs in the crevices. It is possible that the soil washed into the crevices is derived partly from the lichened surfaces and that ultimately the shrubs colonise the slabs from the edges. Thus the lichen stage is replaced, not by a new development on the surface, but by a marginal encroachment of a later stage, to which however the lichen stage has contributed (phot.2).

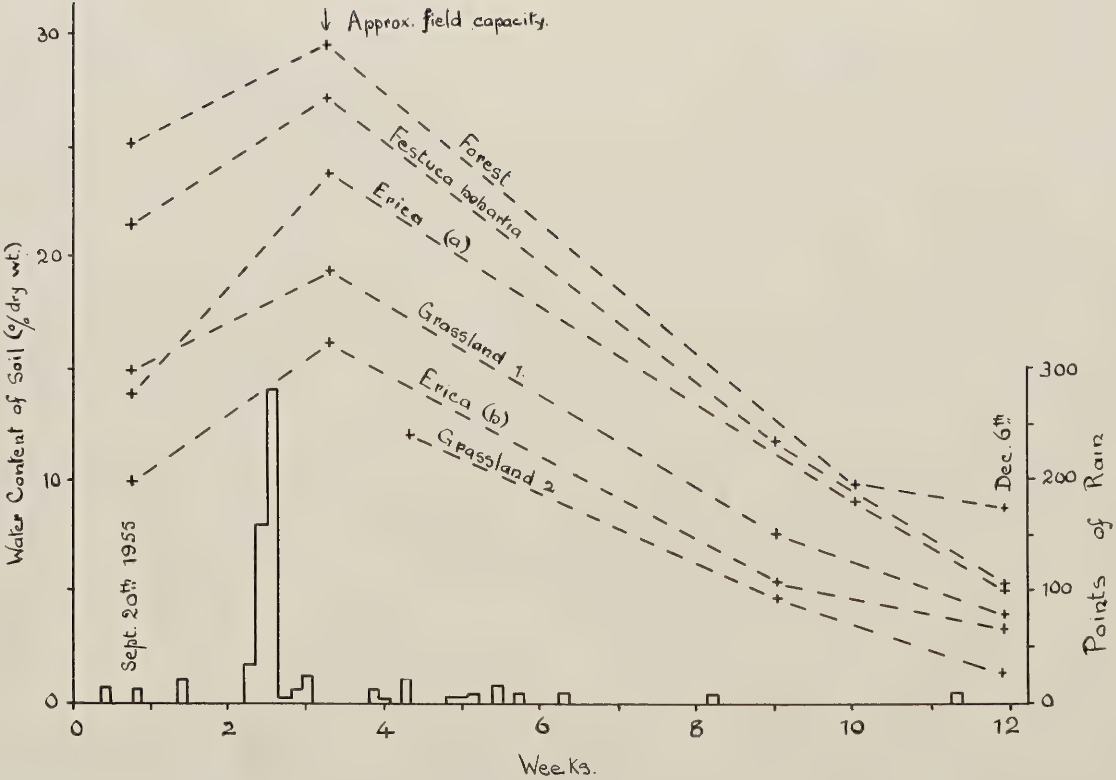
The woodland too is essentially physiographically controlled. Of the three main forest sites on the Reserve, the smallest is on a gentle slope lacking shelter, but apparently with a high water table due to the drainage from above being impeded by a rock barrier. The second area lies along the stream feeding Featherstones Kloof and the tallest woodland in this is simply a narrow strip along the stream. This site owes its existence partly to the higher availability of water, partly to shelter by the steep slope behind it. The smaller foci in which *Rapanea*, *Rhus legati* and other woodland pioneer species are developing are also mainly restricted to these two types of site.

The area to the east of Dassie Krantz is the most difficult to account for, since it appears to be unrelated to special conditions, either of shelter or ground water. It cannot easily be interpreted as cloud forest, for despite its higher altitude, a good deal of heath and grassland exists with the same altitude, and it is doubtful if cloud ever develops in sufficient quantity on the slope to give rise to sufficient precipitation. Liebenberg (1933) reported experiments on this area with vegetation screens, showing a supposed high "induced" rainfall, due to interception by tall plant cover of 62% extra precipitation at 4 ft. and 105·2% at 20 ft., but this in itself would not be sufficient to account for the development of woodland on this section of the slope, rather than elsewhere, even if the interpretations themselves were free of criticism (Fourcade, 1942). The ease with which trees colonise boulder talus and rock faces may form a clue. The soils of the woodland are mainly particularly shallow with a great many boulders at the surface. The slope is above average for the Reserve (up to 40°, phot 11). Only trees appear capable of effectively colonising such terrain, as their root systems are widespread and deep-growing enough to penetrate the talus for a firm anchorage, and obtain water from the inner part of the talus. Judging by the luxuriance of the vegetation on the Dassie Krantz talus, the water content not far below the surface must be high. The conclusion would thus be that trees occupy much of this area only because no other vegetation could colonise it effectively. If this is so, this area of forest is not necessarily the end point of a sere leading through heath, but may be a community climaxing a sere beginning on bare boulder scree, capable however of spreading laterally from this centre into adjacent heath.

Table II shows that the soil organic content (measured as loss on ignition) in forest is twice that of the heath. At the time of sampling (shortly after heavy rain with soil close to field capacity) the water content was also roughly twice that of the heath. The pH is closer to neutrality and the nitrifying power high, indicating higher base status and fertility. Samples from the stream bank community and the Dassie Krantz talus, both potential forest sites, also have some of these properties, suggesting that the forest may not necessarily create these soil conditions, but may invade sites where they already exist, at least in part. Text fig. 8 shows that forest soil, both in wet and dry climatic conditions, possesses a higher water content than heath or grassland soils. The surface soil of forest, none the less, initially loses water rapidly after rain. Probably both transpiration and drainage are rapid, yet as the soil dries out water tends to be conserved, owing partly to the higher humus content, partly to the lower direct evaporation loss, partly to the ability of the trees to exploit deeper levels of the soil for water as the surface layers dry.

2. Life form spectrum and physiognomy.

The Raunkiaer life-form spectrum of the Reserve is interesting. Despite the domination of parts of the area by heath and forest, it is noteworthy that all the phanerophytic classes, even nanophanerophytes, are below the average of



TEXT FIG. 8.—Twelve week survey of water content of surface soil at six sites in five community types, in which time water content fell from near field capacity to near wilting point, illustrating the relatively high rate of loss from forest soil, and the marked overlap between heath and grassland.

the normal spectrum. Epiphytes are not very conspicuous, therophytes would be even less significant if introduced casuals and ruderals were excluded. They form an insignificant part of the natural flora. The spectrum is dominated by chamaephytes, hemicryptophytes and geophytes. The flora of the Reserve is representative of the vegetation of a large part of Central Albany, and there is no reason to think that the addition of another 200 species (representing species typical of this flora but not present in the Reserve) would appreciably alter the composition of the spectrum. Such a spectrum is difficult to match, and resembles most closely the spectra of certain kinds of grassland and steppe.

Table XX

LIFE FORM SPECTRA

	MM	M	N	Ch	H	G	HH	Th	E	Pt.Q	No. spp.
Grahamstown											
Nature Reserve	5·2	8·5	11·7	**18·8**	36·6	11·1	2·0	5·4	1·2	0·9	691
Normal Spectrum	8	18	15	9	26	4	2	13	3	1·0	1000

The term "sclerophyll" has been used (Adamson, 1938) to describe the vegetation of the Western Cape, to which the heaths of Albany are floristically related. The sclerophyll leaf, cartilaginous, xeromorphic, but flat and of moderate size (of microphyll or mesophyll size class) is not however so characteristic of the heaths of Albany. Proteaceae, e.g. *Protea* and *Leucadendron* spp., which make up a large part of the Cape sclerophyll, together with plants of similar habit such as *Gymnosporia laurina*, are not a major part of this vegetation. The dominant nanophyllous and leptophyllous heath species are replaced in succession (in those areas where heath does not itself represent the climax) by the precursors of forest. The forest species are predominantly microphylls and mesophylls but for the most part not strongly sclerophyllous. The term "notophyll" (Webb, 1959) defines the leaf size class which, on Raunkiaer's grouping comprises small mesophylls. To this size group a very large number of the forest species of Albany belong. Of 44 trees and woody lianes entering canopy in forest of the Reserve, I estimate 18 to have microphylls, 22 notophylls, 3 mesophylls (sensu Webb) and 1 macrophyll.

The abundance of the chamaephytes, hemicryptophytes and geophytes in the heath probably reflects in some part the long-standing prevalence of fire in these communities. Du Rietz (1931), in a critical review of the life-form concept, proposed some revision of the chamaephyte concept of Raunkiaer. His classification of shrub life-forms is more penetrating than that of Raunkiaer. It is interesting that two of the categories recognised by him—the dwarf shrub (holoxyle) and half-shrub or suffrutex (hemixyle) are very common on the Reserve. If Du Rietz were to be followed in putting the chamaephyte limit at 0·8 m instead of Raunkiaer's 0·25 m, the greater part of the heath, even many of the dominants, would be classified as chamaephytes. More important than the precise delimitation of the chamaephyte level, is the fact that, among the hemixylic and holoxylic groups the erect aeroxylic (persistent aerial stem, branching near base) and geoxylic (non-persistent aerial stems, branches developing from hypogeal mesocorm stock or lignotuber) types are commonest. Of the aeroxylic type, Du Rietz says "I do not know of a single example of a North European dwarf shrub species regularly belonging to it. On the other hand, this is one of the most common types of dwarf shrub in the heath vegetation of the southern parts of Australia, and probably also in other regions with a similar climate (e.g. the Cape)."; of the geoxylic type "(This) type is about as common as the aeroxylic type (in Australian heath vegetation)". Lignotubers occur also in some true shrubs, e.g. *Protea cynaroides*. Du Rietz' supposition about the Cape is evidently correct, as far east as Albany.

It is the geoxylic type of dwarf shrub (e.g. *Leucadendron salignum* and *Struthiola* spp.) and half shrub (e.g. *Chaetacanthus setiger* and *Indigofera* spp.) which are most abundant on the Reserve and this type which is so well pre-adapted to fire. As the climatic limits of the South African heath (just as in the Australian heath) are approached, so the larger microphanerophytes and nanophanerophytes diminish in numbers, to be replaced by these fire-hardy forms. Finally, grasses and other hemicryptophytes replace the woody life-forms as the climatically favoured types. The winter rainfall of the Cape is both heavy and extremely reliable and fires occur mainly in summer. At Grahamstown both winter and summer rainfall are unreliable and fires frequently occur in winter. Liebenberg's analysis (l.c.) shows the summer rainfall to be more reliable than the winter. Jarrett and Petrie (1929) argued against the view that fire-favoured life-forms represented a direct adaptation to the survival of fire. They pointed out that certain fire-resisting characters are also found in plants of regions not subject to fire. Allowing that some characteristics which enable plants to survive fire may originally have been selected for other functions, I see no reason why this should be supposed of the geoxylic habit. If the geoxylic habit is resistant to fire, then assuming that fire has been a factor in the history of the vegetation of some climatic regions for a very long time, natural selection would favour the spread of those plants in a species having this habit. If life-forms have adaptive significance at all, this must be the mechanism of their evolution. But if fire has not selected this life-form, to what other feature of the climate is it an adaptation?

The manner in which the lower-growing life forms occur in mature heath suggests that only the periodic destruction of this heath enables them to persist